

SOURCE-SINK DYNAMICS INDUCED BY HUNTING:
CASE STUDY OF CULPEO FOXES
ON RANGELANDS IN PATAGONIA, ARGENTINA

By

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"...que nos digan adonde han escondido las flores,
que adornaron las calles persiguiendo un destino..."

V. Heredia, 1984

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Abstract of Dissertation Presented to the Graduate School
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ON RANGELANDS IN PATAGONIA, ARGENTINA

By

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Source-sink dynamics have been proposed as models to explain population processes on some complex landscapes. However, landscape complexity due to hunting by humans has not been considered explicitly as a mechanism resulting in source-sink patterns. In this study I tested the source-sink model on a hunted population of culpeo foxes (Pseudalopex culpaeus) in Argentinean Patagonia.

The spatial distribution of hunting on culpeos in northwest Patagonia is heterogeneous because large (ca. 200 km²) sheep ranches (where culpeos are hunted for their fur

and to reduce predation on sheep) are interspersed in a mosaic with cattle ranches (where hunting is banned by owners). I studied the population dynamics of culpeos on two cattle and four sheep ranches between 1989 and 1996 and tested predictions about survival, fecundity, and dispersal by monitoring densities, collecting carcasses from hunters, and radiotracking 44 culpeos. I concluded that culpeo populations on sheep ranches could not persist via internal population mechanisms and must be maintained by constant immigration from cattle ranches.

I used simulation tools to evaluate the management implications of my conclusions about culpeo population dynamics. The mosaic of sheep and cattle ranches is dynamic because ranchers switch activities occasionally in response to sheep and wool prices. The current percentage of land on cattle ranches in the region is ca. 37%. According to estimated vital rates of culpeos and landscape structure, the current hunting pressure on culpeos in the region would not be sustainable if that percentage fell below ca. 30%.

A significant modification of the Patagonian steppe ecosystem, apart from hunting, has been the introduction of a large number of exotic species such as the European hare

(Lepus europaeus) and red deer (Cervus elaphus). These species are important prey for native carnivores, including the culpeo. I studied the relative biomass of introduced and native herbivores and omnivores and the food habits of culpeos and other carnivores. Native herbivores and omnivores represented ca. 6% of the biomass of potential carnivore prey, and similar or smaller percentages of carnivore diets. I concluded that native large-bodied species are ecologically extinct as prey of native carnivores in this region of Patagonia.

CHAPTER 1 INTRODUCTION

The structure of landscapes can have profound effects on the population dynamics of species that inhabit them (Dunning et al., 1992; Hanski and Gilpin, 1996). Landscape structure is determined by the physical layout and relative amount of different habitat types or patches (Turner, 1989) and by the connectivity among patches (Taylor et al., 1993). Some landscape patches can be recognized by natural or human-created discontinuities of habitat features, like plant cover, that are obvious to the human eye. However, other habitat features that can vary across the landscape, such as the level of predation pressure, can be harder to recognize. In many animal populations hunting is an important source of predation pressure.

The effect of hunting by humans on ecological patterns and processes at a landscape scale has been largely ignored in recent ecological research. Hunting by humans can lead to extirpation of entire faunal assemblages even in ecosystems where the habitat appears to be relatively intact

(Redford, 1992). The presence of humans is ubiquitous in most non-protected and many protected landscapes. However, land tenure, land-use practices, and natural habitat heterogeneity result in a heterogeneous distribution of hunting throughout the landscape. Evaluating the effect of spatial complexity of hunting on the population dynamics of species under intense hunting pressure is an unexplored area of research that deserves attention, both for its ecological and conservation implications.

The Patagonian steppe of southern Argentina and Chile is a mixed shrub-grassland ecosystem where the main economic activity of humans is livestock raising. This ca. 450,000-km²-area appears relatively undisturbed, except for the presence of sheep and cattle and the reduction of plant cover and alteration of soil structure due to grazing. Habitat degradation is more pronounced in areas grazed by sheep than by cattle, due to different grazing patterns and livestock densities.

Sheep and cattle ranches are intermixed in a mosaic-type arrangement in northwest Patagonia. This mosaic is due to differential productivity of pastures (with cattle ranches being more common on more productive lands and sheep

ranches predominating in poorer pastures) and to decisions by land owners based on factors ranging from historical and current prices of wool and beef to the need to reduce degradation of pastures and improve habitat for wildlife to facilitate sport-hunting by owners.

In addition to livestock raising, two other human modifications have probably produced significant changes to ecological patterns and processes throughout the region. First, exotic herbivores (European hare, Lepus europaeus, rabbit, Oryctolagus cuniculus, and red deer, Cervus elaphus) were introduced during the late 1800s and early 1900s (Grigera and Rapoport, 1983; Funes, 1996). These herbivores have reached high densities and in the case of hares have colonized most of Argentina and part of Chile. The second major human impact is widespread hunting of wildlife by local people for commercial and subsistence purposes. Hunting is done mainly by poor rural workers at large sheep and cattle ranches, and to a lesser extent by Mapuche Indians on state-owned lands and by inhabitants of small towns. Wildlife of commercial value includes native furbearers (mainly culpeo, Pseudalopex culpaeus, and chilla foxes, P. griseus) and introduced hares and rabbits.

Furbearer hunting is done in winter when pelts are prime and represents 4 to 26% of the annual income of local people (Novaro, 1995). Exports of furs of chilla and Pampas fox (P. gymnocercus) from Argentina averaged 460,000 annually between 1975 and 1985 (Garcia Fernandez, 1991). Hunting for subsistence supplements protein intake and concentrates on native herbivores and omnivores like guanacos, rheas, armadillos, and mountain viscachas (Novaro and Funes, unpublished data).

This study focuses on the direct and indirect effects of human activities on culpeo-fox populations in northwestern Patagonia. The culpeo fox was chosen because it occurs in large numbers throughout most of the region, the sale of its fur represents a significant source of income to local people, and hunting of culpeos is spatially heterogeneous because it is only conducted on sheep ranches and not on cattle ranches.

The main direct effect of human activities on the culpeo is increased mortality due to hunting, which is concentrated on sheep ranches. Culpeos prey on sheep and are considered the main source of loss of productivity by sheep ranchers (Bellati and von Thungen, 1990). Therefore

ranch owners encourage culpeo hunting by their workers and supplement the workers' income when fur prices decline (Novaro, 1993). In contrast, owners of cattle ranches ban culpeo hunting by their workers because this fox preys intensively on hares (Crespo and de Carlo, 1963; Johnson and Franklin, 1994a; Novaro, 1991), which are thought to compete for forage with livestock. Therefore, the spatial distribution of hunting on culpeos creates a mosaic of hunted and unhunted patches on sheep and cattle ranches. The impact of this hunting pattern on the population dynamics of culpeos was the focus of the main part of this dissertation.

The main indirect effect of human activities is the modification of the prey base for culpeos and other carnivores. Most studies of carnivore food habits and their prey base in the region (reviewed in Medel and Jaksic, 1988, and Novaro, 1997) have been conducted in protected areas, where the prey base is relatively unchanged. However, the use of these carnivores as furbearers, and of the culpeo fox in particular, occurs outside of protected areas. Almost no information is available on predator-prey interactions or overlap among carnivore diets outside of protected areas.

This information is essential to make management recommendations for culpeos, because it provides knowledge about the culpeo ecology and helps understand their role as sheep predators. A description of the prey base of culpeos and other carnivores, and of their prey selection, was the secondary goal of this dissertation.

I analyze the implications of the spatial complexity of hunting on the population dynamics of culpeos in Chapter 2. I studied demographic parameters of culpeos on hunted and unhunted ranches to evaluate two hypotheses: 1. that the population dynamics of culpeos is dominated by a source-sink pattern (Pulliam, 1988), where sink populations (on sheep ranches) are maintained by immigration from sources (cattle ranches), and 2. that the population dynamics of culpeos are dominated by intra-patch (sheep or cattle ranch) processes (reduced natural mortality or increased fecundity) that allow populations to persist in spite of high hunting pressure. In Chapter 3 I use a simulation method to analyze the research and management implications of my conclusions on the population dynamics of culpeos.

In a series of appendices (I-VII) I present additional information from my study on culpeo foxes. In the last

appendix (VII) I present results of density estimations of culpeo foxes and evaluate methods used in these estimations. Management plans of furbearers in Patagonia (Novaro and Funes, 1994) use methods to estimate relative densities that need to be calibrated to determine whether indices of relative densities accurately reflect absolute densities (Lancia et al., 1994). I conducted a calibration of the scent-station method to estimate densities of culpeos and present estimates of culpeo density combining captures and movement patterns evaluated with radiotelemetry.

Finally, in Chapter 4 I describe the current composition of the prey base available to culpeos in northwestern Patagonia, resulting from the introduction of exotic herbivores and domestic species. I also describe the food habits of culpeos and other carnivores, and analyze their patterns of prey selection. I centered the selectivity analysis on comparing biomasses ingested with biomasses available of each prey. Previous studies of carnivore food habits in the region that used frequencies of occurrence of prey items (reviewed in Medel and Jaksic, 1988) may have underestimated the importance of larger prey, including most domestic and exotic species.

CHAPTER 2
SOURCE-SINK DYNAMICS OF A HUNTED CULPEO-FOX POPULATION
IN NORTHWESTERN PATAGONIA

Introduction

The composition and spatial arrangement of habitat patches in the landscape affect ecological processes that can have a strong influence on the population dynamics of species (Dunning et al., 1992). One of the processes affected by landscape complexity is the source-sink dynamic produced when individuals in the same population occupy habitat patches of different qualities (Lidicker, 1975; Pulliam, 1988). Productive patches act as sources of emigrants, which disperse to less productive sink patches. Subpopulations in the sink habitat would go extinct without the rescue effect (Brown and Kodric-Brown, 1977) of immigrants from sources. Few empirical studies have described populations with source-sink dynamics (Hanski and Simberloff, 1996), and all of these studies have focused on natural heterogeneity in habitat quality.

Hunting by humans is a widespread ecological process affecting animal populations in most non-protected landscapes. Hunting usually concentrates on areas that are more accessible to humans or where land use and land tenure make it feasible. Thus hunting may be a strong determinant of habitat quality for game species and may significantly influence their population dynamics at a landscape scale.

Intensively hunted populations of furbearers with high dispersal ability may persist due to immigration from unhunted areas. This demographic pattern resembles a source-sink dynamic and has been suggested for populations of coyotes (Canis latrans; Pyrah, 1984), red foxes (Vulpes vulpes; Allen and Sargeant, 1993), bobcats (Lynx rufus; Knick, 1990), and lynx (Lynx lynx; Slough and Mowat, 1996; Ward and Krebs, 1985) in North America. Animal populations with source-sink dynamics can be stable even if only a small fraction of individuals occupy source areas (Pulliam, 1988). If harvested populations persist mainly via source-sink dynamics, then management for sustainable use must be implemented at a regional scale and include unhunted refugia. However, harvested populations may also persist via demographic processes within a hunted patch of habitat.

These processes may include increased fecundity or reduced natural mortality due to density-dependent effects (Sinclair, 1989). If harvested populations persist mainly via intra-patch population processes, management for sustainable use must focus on the local scale and concentrate on regulating the size of the harvest.

Culpeo foxes (Pseudalopex culpaeus) are intensively hunted in Argentinean Patagonia for their fur and to reduce sheep mortality (Bellati and von Thungen, 1990; Novaro, 1993). The impact of hunting on foxes in Argentina is unknown, and the I.U.C.N. Canid Specialist Group (Ginsberg and Macdonald, 1990) has recommended studies of the culpeo to determine whether exploitation of this species is sustainable.

The spatial distribution of the hunting pressure on culpeos in northwestern Patagonia is highly heterogeneous. Cattle ranches (where hunting is banned by owners because the culpeo preys intensively on European hares, Lepus europaeus, which may compete for forage with livestock) are intermixed with sheep ranches (where owners promote hunting to reduce predation on sheep; Novaro, 1991, 1995). Ranch size ranges between 80 and 600 km², but most ranches are ca.

200 km² in size. A comparison of indices of culpeo density pre- and post-hunting season in 1989 indicated that densities declined by an average of 74% at five hunted sheep ranches but changed only 10% at two unhunted cattle ranches (Novaro, 1991, 1995). Furthermore, simulations of culpeo population dynamics with age structure and reproductive data from a sheep ranch in the same area but collected 30 years earlier (J. A. Crespo, unpubl. data; Crespo and de Carlo, 1963) indicate that hunted populations could not sustain current levels of harvest and eventually should collapse (Novaro, 1995). However, these hunted populations did not decline over three decades in spite of the continuous hunting pressure. Surveys after 1989 indicated that 1) hunted populations recovered by the beginning of each hunting season, that 2) the number of culpeos harvested on the five sheep ranches was larger in 1990 than in 1989, and that 3) regional harvest has changed little during the last three decades (Novaro, 1991, 1995).

The demography of culpeos may be determined by a mosaic of sources and sinks (Pulliam, 1988; Pulliam and Danielson, 1991) created by differential mortality due to hunting. However, alternative explanations such as a strong density-

dependent response within hunted populations have not been examined. The purposes of this study were to describe the population dynamics of harvested culpeos, test hypotheses about the mechanisms that allow their populations to withstand high hunting pressure, and provide management recommendations for the sustainable use of culpeos in northwestern Patagonia.

Hypotheses about Impact of Hunting on Culpeos

I examined two alternative hypotheses to explain the population dynamics of culpeos due to the effect of hunting:

H₁: The heterogeneous spatial distribution of hunting produces a mosaic of sources and sinks (Pulliam and Danielson, 1991) that allows culpeos to persist in hunted areas. Population recovery each year in hunted areas is due to immigration of surplus individuals from unhunted areas where recruitment exceeds mortality.

H₂: Internal population mechanisms allow culpeos in hunted areas to sustain high harvest pressure and recover after each hunting season. Recovery may occur through a density-dependent response by an increase in the reproductive rate and/or a decline in natural mortality rate (Caughley and Sinclair, 1994).

Under H_1 the dynamic of the culpeo population is determined by the links among patches (hunted and unhunted areas). If the sink-source model fits the culpeo population data, density-dependent responses in reproduction or mortality could occur in sinks but would be insufficient to compensate for the high hunting mortalities. If this hypothesis were correct, management for sustainable use should concentrate on maintaining the spatial heterogeneity of land uses that allows the existence of harvest refugia.

Under H_2 internal population processes within each patch explain the culpeo population dynamics. Culpeos in hunted areas may have high reproductive rates or low natural-mortality rates that could compensate for hunting mortality. High reproduction or low natural mortality could be due to higher availability of resources to breeding pairs at the end of each hunting season (because of reduced culpeo population density) and/or inherent higher abundance of certain prey (e.g., hunting occurs mainly on sheep ranches and sheep are an important prey of culpeos; Novaro, 1991; Chapter 4). If this hypothesis were correct, management for sustainable use should concentrate on maintaining culpeo productivity in hunted areas.

Predictions Tested

I attempted to test the following predictions of the source-sink hypothesis, which, if false, would suggest internal population processes are more significant than links among patches in the culpeo population dynamics (Table 2-1):

Prediction 1. Survival rates of culpeos are significantly lower in hunted than unhunted ranches.

Prediction 2. Fecundity rates are similar in hunted and unhunted ranches.

An assumption of the source-sink hypothesis is that prey productivity was similar on sheep and cattle ranches. If prey productivity was lower on sheep ranches, lower food availability could explain lower culpeo survival or fecundity rates on sheep ranches. Densities of the main prey of culpeos, the European hare, of other prey such as rodents and edentates, and biomass of carrion were similar on sheep and cattle ranches (Aubone et al., 1996; Corley et al., 1995; Novaro et al., 1992; Chapter 4). Only the availability of sheep varied significantly between the two types of ranch. Thus I did not expect differences in prey

Table 2-1. Summary of predictions under hypotheses of dominant dynamics of culpeo populations. UH: un hunted ranches; H: hunted ranches.

Predictions:	Dominant dynamics	
Process	H ₁ : Source-sink	H ₂ : Intra-patch
1.Survival	UH >> H	UH = H
2.Fecundity	UH = H	UH << H
3.Rate of increase(lx,mx)	UH >> H	UH = H
4.Dispersal scale	between patches	within patches
5.Dispersal direction	to UH << to H	to UH = to H
6.If hunting stops on H, natural mortality compensates hunting mortality	No	Yes

productivity between ranches to account for patterns of survival and fecundity observed.

Prediction 3. The rate of increase (r) of the culpeo population based on the schedules of survival and fecundity is significantly <0 on hunted ranches and significantly >0 on unhunted ones, but the observed rates of increase are not significantly different from 0 on both types of ranches if the regional population level is stable. Prediction 3 is not independent from Predictions 1 and 2, but it rather integrates information from those predictions into one demographic parameter (r).

Prediction 4. Most culpeos disperse across distances large enough to migrate between ranches. The diameter of most ranches (ca. 200 km² in size) is ca. 16 km. If most culpeos disperse farther than 16 km they would establish new ranges on a different ranch from their natal one.

Prediction 5. Dispersal rates into unhunted ranches are significantly lower than into hunted ranches. If direction of dispersal were random, the ratio of culpeos establishing new ranges on unhunted to hunted ranches would be equal to the ratio of area on unhunted to hunted ranches in the regional landscape.

The study was conducted on six ranches in southern Neuquén Province, Argentina, between May 1989 and March 1996. Two of the ranches were un hunted and four were heavily hunted. Due to logistical difficulties, predictions on survival and dispersal were tested on only one un hunted and an adjacent hunted ranch. Culpeo hunting was banned on this hunted ranch during the second year of the study so a sixth prediction from the sink-source hypothesis was tested:

Prediction 6. If hunting mortality is removed from a previously hunted ranch, culpeo survival will increase significantly because any increase in natural mortality would not be sufficient to compensate (Caughley, 1977) for hunting mortality.

Materials and Methods

Study Area

The study area was located in the vicinity of the town of Junin de los Andes (40°S, 71°W) in northwestern Patagonia, Argentina. Sheep and cattle production in large ranches (18,000 to 27,000 has) are the main economic activities. Six ranches were chosen to represent dominant land-use types in the region. Cattle raising is the main activity at Collun Co ranch, sheep raising predominates at

Catan Lil, La Papay, and Cerro de los Pinos ranches, and cattle and sheep are raised at La Rinconada and Los Remolinos ranches. Culpeo hunting pressure was low or non-existent at Collun Co and La Rinconada and high at the remaining ranches. Prior to 1994, all ranches had maintained consistent management practices with respect to hunting and livestock for at least 80 years. However, in 1994 the owners of Cerro de los Pinos sold 90% of their sheep and banned fox hunting. The total area of all six ranches was 1,420 km² (33% on cattle and 67% on sheep ranches; Figure 2-1). About 37% of land in the surrounding region (ca. 5,000 km²) was cattle ranches (Chapter 3).

The region falls within the Patagonian Phytogeographic Province, Occidental District (Cabrera, 1976). The vegetation is characterized by a mixed steppe of grasses and shrubs and dominant species are Mullinum spinosum, Senecio sp., Stipa sp., and Poa sp.

The weather is dry and cold, with frosts throughout the year and frequent snowfalls in winter. Mean, mean highest, and lowest annual temperatures were 11, 17.4, and 2.5°C, respectively. Mean annual rainfall ranged from 28 cm to 75

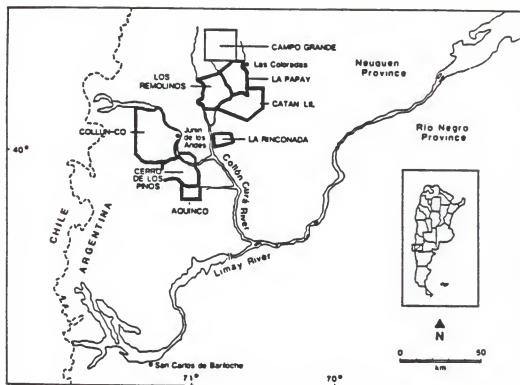


Figure. 2-1. Study area in northwest Patagonia, Argentina. The thick lines indicate the borders of the ranches studied. Crespo and de Carlo (1963) conducted a study of culpeo age structure and reproduction in Campo Grande ranch.

cm at different ranches, and was primarily concentrated during the winter.

Topographically the study sites consisted of great plains 800 to 900 m above sea level, dissected by steep, rugged canyons and valleys. In the bottom of the valleys there were areas with moist soil and dense herbaceous vegetation, called "mallines," where the dominant species were Cortadeira araucana, Juncus sp., and Carex sp. These areas have high primary productivity (Movia et al., 1982).

Short-term Study of Survival and Dispersal

I studied survival and dispersal of culpeos with radiotelemetry on Collun Co (control) and adjacent C. de los Pinos (hunted) ranches between January 1, 1993, and March 15, 1996. Between January and May of 1993 and 1994, culpeos ($n = 47$) were captured with padded leg-hold traps (Victor coyote-size soft-catch coil spring; Johnson and Franklin, 1994b) and anesthetized with ketamine hydrochloride (Ramsden et al., 1976; approximate dosages 10-25 mg/kg body weight). Trapping caused only swelling of the trapped foot, and swelling had disappeared by the time culpeos were released. Trapped culpeos were measured, sexed, weighed, checked for general physical condition, ear-tagged, and an estimation of

age taken based on tooth wear (Crespo and de Carlo, 1963; Zapata et al., in press). Adults ($n = 23$) and juveniles ($n = 21$) that weighed at least 50% of adult body-mass (approximately 4 months old; Crespo and de Carlo, 1963) were fitted with radio-collars (A.T.S. Inc., Isanti, Minnesota) weighing up to 5% of body mass. Animals were released at the capture site following recovery from anesthesia.

Culpeos were fitted with radio-collars as follows: control, 1993 - 11 foxes, 1994 - 10 foxes; hunted ranch, 1993 - 16 foxes, 1994 - 7 foxes. Thirty different culpeos were radiotracked in 1994 due to survival of individuals during 1993 (Appendices I and II). During 1995 and 1996 I monitored only 18 culpeos radiocollared during 1993 and 1994 (Appendix III). Sixty-two and 36 percent of culpeos radiocollared on the hunted and unhunted ranches, respectively, in 1993 were juveniles (Appendix I). Seventy-one and 60% of culpeos radiocollared on the same ranches in 1994 were juveniles (Appendix II). Fifty percent of radiocollared culpeos were females.

Radio-collared animals were tracked from a vehicle and occasionally from a fixed-wing aircraft, approximately twice every week for up to three years or until they died

(Kenward, 1987; Harrison, 1992). Radio-collars had an inscription asking hunters to return them and the culpeo's carcass if encountered. Interviews of hunters were conducted to establish date, location, and method of kill and carcasses were necropsied to determine cause of death. Ages of radio-collared culpeos that died were determined using the cementum annuli technique (Root and Payne, 1984; Zapata et al., in press).

Dates of capture and death of culpeos were used to estimate daily survival rates and 95% confidence intervals in each population with the Kaplan-Meier method (White and Garrott, 1990). Survival rates of juvenile and adult culpeos were different, so they were analyzed separately. On average, culpeos were captured 79 and 81 days after January 1 in 1993 and 1994, respectively. Thus yearly survival rates of adults were estimated between 15 March of one year and 14 March of the following year (Appendices I, II, and III). Survival rates of juveniles were estimated between 15 March and 15 November (the mid point of the birth pulse of culpeos, Crespo and de Carlo, 1963) of each year. Survival rates in 1994 were based on the new animals collared that year plus surviving culpeos from 1993.

Survival rates were compared between the hunted and unhunted population using the log-rank test in program SAS (SAS Institute Inc., 1996) with the program provided by White and Garrott (1990).

Some culpeos dispersed from C. de los Pinos and Collun Co to other hunted and unhunted ranches. Survival data of culpeos on these other ranches was grouped with data from C. de los Pinos or Collun Co according to the hunting pattern of each new ranch. Thus all survival data presented corresponds to populations on all hunted or unhunted ranches combined. Animals that moved from one ranch to another were considered censored (White and Garrott, 1990) from the first ranch and were added to the second one if the hunting patterns of both ranches were different. Due to dispersal of culpeos between ranches with different hunting patterns, a total of 19 and 12 culpeos were radiotracked on hunted and unhunted ranches, respectively, in 1993 (Appendix I). During 1994, 13, 2, and 19 culpeos were radiotracked on formerly hunted, hunted, and unhunted ranches, respectively (Appendix II).

Fecundity was calculated as the product between the proportion of pregnant females and the number of female pups

produced by each breeding female (Caughley and Sinclair, 1994). Data from radiotracked females ($n = 8$) and from carcasses obtained from hunters ($n = 87$, see Long-term monitoring of population parameters) were combined to estimate proportion of pregnant females and litter size on hunted ranches. Only radiotelemetry data ($n = 10$ females) were used to estimate proportion of breeding females on unhunted ranches. Females with radiocollars were identified as breeding if they denned and if pups or their signs were observed. Pup counts at the den (Gese et al., 1989) were used also to estimate litter size of radiocollared and non-collared females.

I attempted to evaluate survival rate of culpeo pups by tagging them at den sites during the 1992-1993 and 1993-94 breeding seasons and recovering tags from hunters (Windberg et al., 1985). Dens were located by radio-tracking females and through information from ranch workers at Collun Co and C. de los Pinos. Culpeos were flushed from their dens (Storm and Dauphin, 1965) and pups were caught by hand or with a dip net or noose when they emerged (Storm et al., 1976). However, only three litters could be tagged and

attempts at 14 other dens were unsuccessful, so the capture of pups was suspended.

I estimated dispersal rates from the proportion of radio-collared culpeos that dispersed into each ranch. I recorded approximate dates of departure from natal range and arrival at new range, dispersal distance, and type of ranch (unhunted or hunted) that contained the new range. The ratio of culpeos that dispersed into unhunted ranches to those that dispersed into hunted ranches was compared to the ratio of land on cattle vs. sheep ranches ($37\%/63\% = 0.59$; Chapter 3) using a randomization test due to small sample sizes (Bruce et al., 1995). Differences were considered significant if $P < 0.05$.

Long-term Monitoring of Population Parameters

I studied culpeo reproductive parameters and age and sex ratios by collecting culpeo carcasses from hunters on all ranches during the hunting season (May through August) between 1989 and 1994. Carcasses were preserved in 5% formalin solution and were sexed, weighed, and checked for general physical condition. Canine teeth were extracted for age determination by counting cementum annuli (Root and Payne, 1984; Nellis et al., 1978). This aging method was

calibrated by determining number of annuli in teeth of culpeos captured as juveniles and radiotracked for one to three years during this study (Zapata et al., in press). Teeth were analyzed at the Donana Biological Station (Sevilla, Spain) and Matson's Laboratory (Milltown, MT).

Three hundred sixty-two culpeo carcasses were collected between 1989 and 1994. Ages of 327 carcasses and of all radiocollared culpeos at the time of first capture were combined for analysis of age structure ($n = 371$). Ages of remaining carcasses ($n = 35$) could not be determined due to loss of canine teeth and poor preservation. Culpeos were grouped into yearly age classes for juveniles and 1- to 6-year-olds, and 7-year-old and older culpeos were grouped into an 8th age class. Proportions of culpeos in different age classes were compared using log-likelihood ratio tests (Sokal and Rohlf, 1995).

Sex of 305 culpeo carcasses and 47 culpeos captured for the radiotelemetry study was determined. Sex of remaining carcasses could not be determined due to decomposition. Sex ratio was compared to a 1:1 ratio using a Chi-square test (Sokal and Rohlf, 1995).

Embryos were counted on female reproductive tracts to estimate litter size (Crespo and de Carlo, 1963). Numbers of corpora lutea in ovaries were determined at the Donana Biological Station to estimate ovulation rate. The proportion of pregnant females was determined as the ratio between the number of females with embryos or corpora lutea from pregnancy and the total number of females collected during the culpeo breeding season (between October and February of each year; Crespo and de Carlo, 1963). Eighty-seven female reproductive tracts of carcasses from all hunted ranches were analyzed for signs of pregnancy and ovulation. No placental scars were found in any utera, suggesting that scars were erased by the formalin used in carcass preservation. Therefore, assessment of reproductive status was based on examination of corpora lutea and follicles in the ovaries and embryos in the utera.

Data on fecundity were combined for hunted and radiotracked culpeos. I included data from six females studied by Crespo and de Carlo (1963) in the estimation of liter size on hunted ranches, because of the small sample size obtained during my study ($n = 20$). Crespo and de Carlo's estimate (5.2 pups; $SD = 1.9$) was larger than my

estimate. In addition, the fecundity estimate on hunted ranches included data from radiotelemetry and carcasses, whereas the estimate on unhunted ranches was only from radiotelemetry. Thus the rates of fecundity (and population increase) for hunted ranches may be an overestimation because not all pregnant females (in the carcass sample) may have given birth to live litters. However, any overestimation of fecundity on hunted ranches would result in a more conservative test of the predictions on fecundity and rates of increase. Proportions of pregnant females and litter sizes were compared using randomization tests between proportions and for differences between means, respectively, due to small sample sizes and lack of independence among samples (Bruce et al., 1995). Differences were considered significant when $P < 0.05$.

Relative densities of culpeos were estimated on all ranches at the beginning of the hunting season between 1989 and 1995 using scent stations (Roughton and Sweeny, 1982). Scent-station indices accurately reflected relative densities of culpeo foxes in the study area (Appendix VII). Forty scent stations (eight lines of five stations each per ranch) were operated along all internal roads and trails of

each ranch during one night in May or June of each year. Between 1989 and 1991, fermented egg powder (FEP) was used as an attractant and placed on a wooden stick at the center of each station (Roughton, 1982; Novaro, 1991). Between 1992 and 1995 I replaced the FEP attractant with fatty acid scent (FAS, Pocatello Supply Depot) placed on a plaster disc, which has the same 10 fatty acids as FEP but is easier to quantify and handle (Roughton, 1982). Stations within a line were 0.4 km apart, and lines were at least 1.3 km apart to ensure independence among sampling units (Novaro, 1991; Roughton and Sweeny, 1982). Data were expressed as mean percentage of scent stations visited on hunted and unhunted ranches ± 1 SE. Scent-station indices were compared among years using the Fisher randomization test (Roughton and Sweeny, 1982).

Exponential Rates of Increase

The exponential rates of increase (r_x) based on the schedules of survival and fecundity of culpeo populations on hunted and unhunted ranches were calculated using Lotka's (1907a,b) iterative equation

$$\sum l_x e^{-rx} m_x = 1,$$

where l_x and m_x are the survival and fecundity, respectively, of each age class x . Survival was calculated using radiotelemetry data for juvenile and adult culpeos. Mean survival rates on Collun Co were calculated with data from 1993, 1994, and 1995. No data were available on pup survival between 0 and 4 months of age so I assumed 100% survival and used the estimated juvenile survival (4 to 12 months of age) on each ranch as annual survival for the first age class. Fecundity rates of 1- to 5-year-olds were treated as constant and I assumed that females older than 6 years of age did not breed on either ranch (Appendix V). Rates of increase were also expressed as finite rates ($\lambda = e^r$, Caughley, 1977).

The exponential rates of increase (observed r , Caughley, 1977) based on population trends of culpeos on hunted and unhunted ranches were calculated with the linear regression method given by Caughley and Sinclair (1994). I used mean scent-station indices for hunted ($\bar{n} = 4$) and unhunted ($\bar{n} = 2$) ranches between 1989 and 1994. Scent-station indices for 1995 were not used in calculations of r because hunting stopped on C. de los Pinos in 1994. I

determined if either observed χ was significantly different from zero using F tests (Sokal and Rohlf, 1995).

Results

Prediction 1--Survival

The comparative analysis of hunted and unhunted areas indicates that survivorship of culpeos is lower on hunted than unhunted ranches. The survival rate of juveniles on hunted ranches during 1993 (8-month rate = 8.3%; 95% CI = 0.0-25.0%; n=10) was significantly lower than on the unhunted ranches during 1993 and 1994 (80.0%; 44.9-100.0%; n=11; $\chi^2 = 6.1$, $P = 0.013$; Appendices I and II and Fig. 2-2). The survival rate of adults on hunted ranches during 1993 through 1995 (annual rate = 55.6%; 95% CI = 28.5-83.2%; n=9) was lower than on the unhunted ranches (73.0%; 54.9-90.1%; n=17) but the differences were not significant ($\chi^2 = 1.3$, $P = 0.25$; Appendices I and II and Fig. 2-3).

Eleven of 19 culpeos radiotracked on hunted ranches were killed by hunters. Hunting (with shotguns and trained dogs) accounted for 90% of the annual mortality of radiocollared foxes on the hunted ranches (9 of 10 deaths) during 1993 and 100% during 1994 and 1995 (2 of 2 deaths; Appendices I, II, and III). No traps were set by hunters

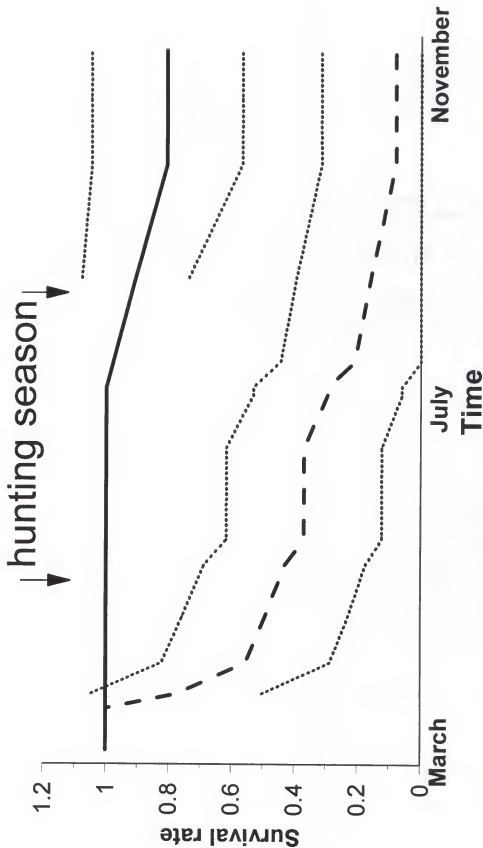


Figure 2-2. Daily survival rates of juvenile culpeos in un hunted (solid line, $n=10$) and hunted ranches (dashed line, $n=10$) between March 15 and November 15 of 1993 and 1994. Dotted lines are 95% confidence intervals. Survival rates were significantly different ($X^2 = 6.1$, $p = 0.01$).

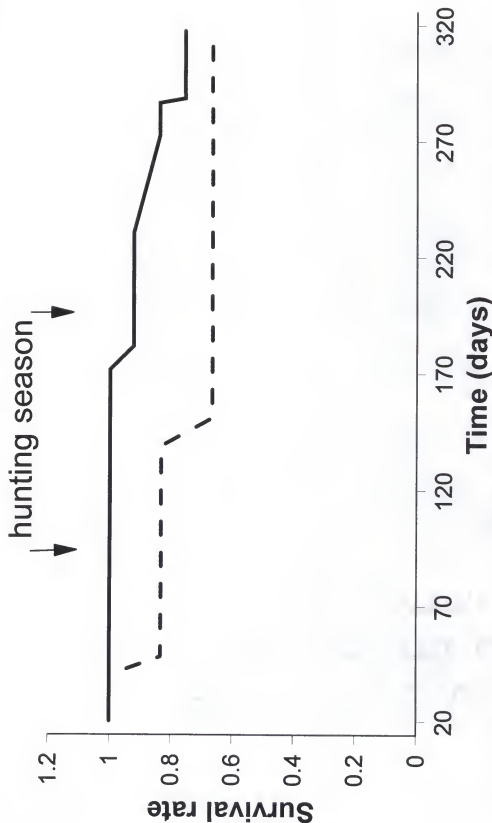


Figure 2-3. Daily survival rates of adult culpeos in unhunted (solid line, n=17) and hunted ranches (dashed line, n=6) between March 15 of each year, during 1993 through 1995. Survival rates were not significantly different ($X^2 = 1.3$, $p = 0.25$).

between 1993 and 1995 due to a decline in pelt prices. The remaining culpeo mortality on the hunted ranches in 1993 was a road kill. On average, culpeos survived only 87 days after being collared or establishing residency on the hunted ranches (Appendix I). Only two juveniles that dispersed from the hunted ranch in 1993 survived (Appendix I). Mortality on the control ranches was due to feral and domestic dogs (6 deaths), poachers (2), puma (Puma concolor; 1), and unknown causes (1; Appendices I, II, and III).

Prediction 2--Fecundity

Litter sizes and proportions of adult females breeding were similar on hunted and unhunted ranches, although sample sizes were small. A detailed description of results is given in Appendix IV. Mean litter sizes of adult females on hunted and unhunted ranches were 4.19 pups (SD = 1.72, n = 26) and 4.25 pups (SD = 0.96, n = 14 dens, Appendices I, II, and IV), respectively. Mean litter size of adult females on hunted ranches excluding Crespo and de Carlo's (1963) data was 3.60 (SD = 1.35, n = 20, combined for 6 reproductive tracts and 14 dens, Appendices I and IV). The proportion of adult females that bred was 0.63 on hunted ranches (n = 8, combined for 5 reproductive tracts and 3 radiotracked

culpeos, Appendix I), 0.75 on unhunted ranches ($n = 8$ radiotracked females, Appendices I, II, and III), and 0.75 on previously hunted C. de los Pinos ($n = 8$ radiotracked females, Appendices II and III). Therefore fecundity rates of adult females were lower on hunted (2.62, $SD = 1.07$; or 2.25, $SD = 0.84$ if Crespo and de Carlo's data are excluded) than unhunted ranches (3.19, $SD = 0.72$), although the difference was not significant (Randomization test, $P = 0.182$).

Litter size of one juvenile female radiotracked during 1993 was 3 (Appendix I). This was the only female that bred during its first year of life on hunted ranches ($n = 5$ reproductive tracts obtained during breeding season). However, the ovaries of three other juvenile females from hunted ranches (of 39 tracts obtained before the breeding season) contained growing folliculi which suggests they were initiating ovulation (Appendix V). Juvenile females radiotracked on unhunted ranches ($n = 4$) and previously hunted C. de los Pinos ($n = 2$) did not breed (Appendices I, II, and III). Four other juvenile females radiotracked were killed and the collar of another one fell before the end of the breeding season. Therefore, insufficient data were

available to determine whether fecundity rates of juvenile females are higher on hunted than unhunted ranches.

The sex ratio used to estimate fecundity of the entire population (males and females) to calculate rates of increase was 1:1. The sex ratio of hunted and radiocollared culpeos was not significantly different from 1:1 (47% female, 53% male ; $\chi^2 = 1.542$; $P > 0.10$). Age distributions were significantly different among ranches ($G = 43.8$, $df = 24$, $P = 0.008$; Table 2-2). The age distribution of hunted populations on C. de los Pinos and Los Remolinos ranches included more juveniles and fewer old culpeos (more than 6 years old) than the unhunted control (Table 2-2). However, age distributions from Catan Lil and La Papay had similar proportions of juveniles as the unhunted ranch. The maximum age of culpeos was 11 years.

Prediction 3--Rates of Increase in Hunted and Unhunted Areas

Based on rates of increase from schedules of survival and fecundity, culpeo populations would be expected to decline markedly on hunted ranches and increase significantly in abundance from year to year on unhunted ranches (Table 2-3). Calculated λ_t during the study period was -0.36 on C. de los Pinos and 0.57 on Collun Co. Thus

Table 2-2. Age structure of live-captured and killed culpeo foxes in a control (Collun Co) and four hunted ranches between 1989 and 1994 in southern Neuquén. Numbers are the percentage of culpeos in each one-year-long age class. Differences among age structures at the sites were significant ($G = 43.8$, $df = 24$, $P = 0.008$).

Age	Control	C.Pinos	C.Lil	L.Papay	Remolinos
0	39.4	58.8	38.6	41.7	59.9
1	9.1	2.5	12.9	6.1	10.8
2	12.1	8.1	20.0	15.7	10.8
3	3.0	8.5	11.4	20.0	7.8
4	9.1	6.5	8.6	11.3	7.8
5	9.1	8.1	5.7	1.7	2.9
6	6.1	1.6		2.6	
7	6.1		1.4		
8	6.1				
9			1.4		
10					
11				0.9	
Sample size	34	93	70	115	36

Table 2-3. Survival rate (p_x), survival (l_x), and fecundity (m_x) of culpeo foxes on hunted and an unhunted ranches in southern Neuquén.

Age	Hunted			Unhunted		
	p_x	l_x	m_x	p_x	l_x	m_x
0	0.08	1.00	0.30	0.50	1.00	0.00
1	0.67	0.08	1.32	0.64	0.67	1.59
2	0.67	0.06	1.32	0.64	0.47	1.59
3	0.67	0.04	1.32	0.64	0.36	1.59
4	0.67	0.02	1.32	0.64	0.27	1.59
5	0.67	0.02	1.32	0.64	0.21	1.59
6	0.67	0.01	0.00	0.64	0.16	0.00
7	0.00	0.01	0.00	0.00	0.12	0.00

finite rates of population increase based on fecundity and survival were -29.9% and 76.8% per year on hunted and unhunted ranches, respectively.

However, culpeo populations remained stable on hunted ranches and increased slightly on unhunted ranches during the study (Fig. 2-4). Culpeo relative densities did not change significantly between consecutive years on either type of ranch (Fisher randomization test, $P > 0.881$) or between 1989 and 1994 on hunted ranches ($P = 0.134$), but increased significantly during these years on unhunted ranches ($P = 0.016$; Fig. 2-4). Observed \bar{x} was 0.09 on hunted ranches (not significantly different from 0, $t = 1.757$, $P = 0.154$) and 0.17 on unhunted ranches (significantly >0 , $t = 3.940$, $P = 0.017$; Fig. 2-4) between 1989 and 1994. Finite rates of population increase were 9.6% and 15.8% per year on hunted and unhunted ranches, respectively. Population trends did not change after 1994: scent-station indices increased slightly (but not significantly, $P > 0.20$) on both types of ranches in 1995 (Figure 2-4).

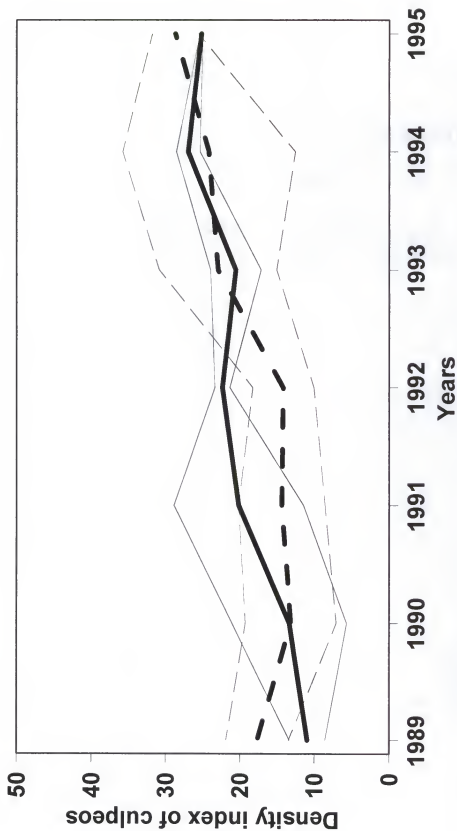


Figure 2-4. Relative densities of culpeos between 1989 and 1995 on two un hunted ranches (solid line; Collun Co and Rinconada) and four hunted ranches (dashed line; C. de los Pinos, C. Lil, La Papay, and Remolinos). Data are mean percentage of scent stations visited (thick lines) and mean \pm 1 SE (thin lines). Population rates of increase between 1989 and 1994 were $r = 0.17$ ($P = 0.02$) on un hunted ranches and $r = 0.09$ ($P = 0.15$) on hunted ranches.

Prediction 4--Dispersal Scale

Dispersal was documented for all juveniles (except two) collared in hunted and unhunted ranches that survived to become one-year-olds (Appendices I and II). Two one-year-old males also dispersed (Appendix I). Most dispersing culpeos established new ranges on a ranch different from their natal one, due to large dispersal distances in relation to ranch size (Figure 2-5). Dispersal distances ranged between 10 and 90 km (Mean = 30.5 km; SD = 29.4; Figure 2-5). One of the 9 culpeos tagged as a pup at a den site dispersed at least 85 km and was shot during the 1995 hunting season. Eight of 11 culpeos for which dispersal distance was recorded migrated between ranches, whereas the remaining three dispersed within the same ranch (Figure 2-5). A detailed description of results is given in Appendix V.

Prediction 5--Dispersal Direction

Direction of dispersal appeared to be non-random (lower rate of dispersal into unhunted than into hunted ranches), but sample sizes were too small to detect a significant pattern. The ratio of the number of radiocollared culpeos

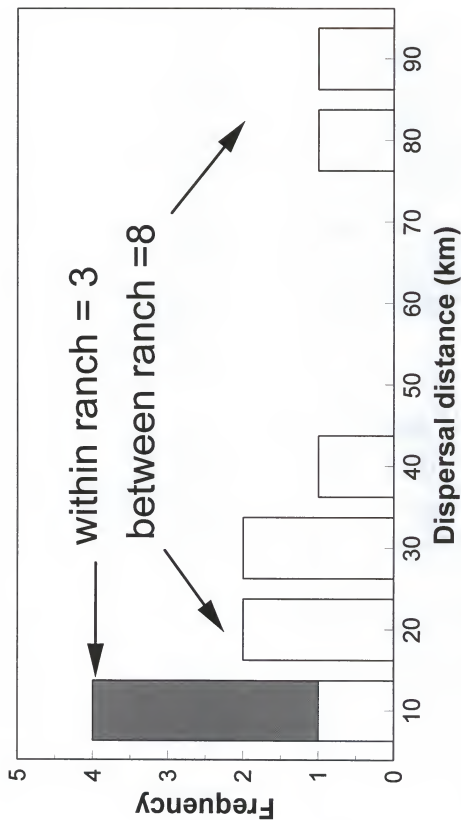


Figure 2-5. Dispersal distances of culpeos radiocollared on a hunted and an unhunted ranch in northwestern Patagonia during 1993 and 1994.

establishing new ranges on unhunted and hunted ranches ($2/5 = 0.4$) was smaller but not significantly different from the ratio of land on unhunted and hunted ranches (0.59; Randomization test of proportions; $P = 0.09$; Appendices I and II).

Dispersal by the culpeo tagged at one den was not included in my analysis as this dispersal event was recorded because the animal was killed on a hunted ranch. Details about direction of dispersal of culpeos are given in Appendix V.

Prediction 6--Compensatory Mortality

Natural mortality and hunting mortality were not compensatory in the culpeo population. Following the removal of hunting in 1994, annual survival rate in formerly hunted C. de los Pinos ranch increased from 31.2% to 83.1% (95% CI = 61.5-100.0%; $n=13$) and was higher, although not significantly different from the control ranches in 1994 (55.5%; 25.5-85.6; $n=17$; $\chi^2 = 1.3$, $P = 0.25$; Appendix II and Figure 2-6). Juvenile and adult survival rates during 1994 were combined because there were no differences between age classes.

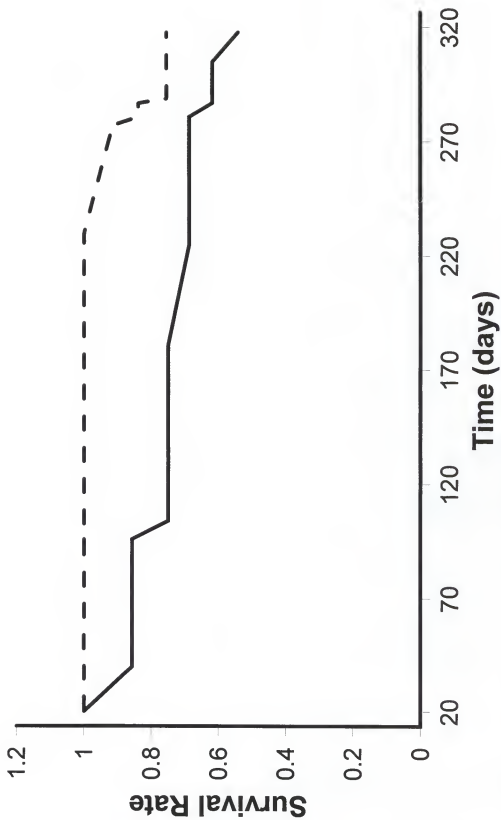


Figure 2-6. Daily survival rates of culpeos during 1994 on an unhunted ranch (solid line; n=13) and a ranch hunted until 1993 (dashed line; n=13).

Differences in survival on C. de los Pinos between 1993 and 1994 were due mainly to increased survival of juveniles. Juvenile survival on C. de los Pinos in 1994 was 83.0% (37.7-100.0%; $n=6$) and was significantly higher than in 1993 (8.3%; $\chi^2 = 6.0$, $P < 0.015$). Survivorship of adults on the previously hunted ranch in 1994 was 83.3% ($n=6$) and on the control ranch was 60.0% ($n=10$; Appendix II). Two deaths of radiocollared culpeos occurred in 1994 on the formerly hunted ranch due to poisoning and unknown causes (Appendix II). The results of the tests of predictions are summarized in Table 2-4:

Table 2-4. Summary of results of tests under hypotheses of dominant dynamics of culpeo populations. UH: unhunted ranch; H: hunted ranch. **: indicates that results were significant ($P < 0.05$); ^{ns}: results were not significant; ?: refers to insufficient data.

Predictions:	Dominant dynamics	
Process	H ₁ : Source-sink	H ₂ : Intra-patch
1.Survival	young: UH >> H ** adults: UH > H ^{ns}	
2.Fecundity	adults: UH = H	young: UH < H ?
3.Rate of increase(lx,mx)	UH >> H	
4.Dispersal scale	between patches	
5.Dispersal direction	to UH < to H ?	
6.Natural and hunting mortality compensatory	No **	

Discussion

In the next sections I discuss the demographic parameters of culpeos and compare them to other hunted carnivores. Then I provide conclusions about the hypotheses on source-sink and intra-patch dynamics. Finally, I discuss the implications of my results for the sustainable use of culpeos.

Tests of Predictions

Results of tests of predictions 1, 3, 4, and 6 supported the source-sink hypothesis. Results for prediction 2 were equivocal, and results for prediction 5 were not considered due to small sample size. Survival of culpeos (mainly of juveniles) was much lower on hunted than unhunted ranches (Prediction 1) and reduced natural mortality could not compensate for the high level of hunting mortality on hunted ranches (Prediction 6). The source-sink hypothesis also was supported by the comparison between calculated rates of increase from schedules of survival and fecundity and observed rates of increase from population trends (Prediction 3, primarily due to low survival on hunted ranches) and the larger proportion of culpeos that dispersed between than within ranches (Prediction 4).

Fecundity of adult females was similar on hunted and unhunted ranches (supporting Prediction 2 from the source-sink model), but fecundity of juvenile females may be higher on hunted than unhunted ranches (supporting Prediction 2 from the intra-patch model). However, contribution of juvenile females to population recruitment on hunted ranches is probably low due to their low survival. In summary, I found little evidence to conclude that the population dynamics of culpeos are dominated by intra-patch processes (like reduced natural mortality or high fecundity) that would allow them to persist under intense hunting pressure.

Survival rates

Tests on fox survival rates in the study area were based on data from culpeos captured only on one hunted and one unhunted ranch. However, population trends observed during the 1989 hunting-season on all five hunted ranches (Figure 2-7; Novaro, 1991) suggest that the pattern of high mortality due to hunting is common. Similarly, population trends on Collun Co and La Rinconada during 1989 (Figure 2-7) also suggest that winter mortality of culpeos on unhunted ranches is low and similar to that recorded on Collun Co during the radiotelemetry study from 1993 to 1995.

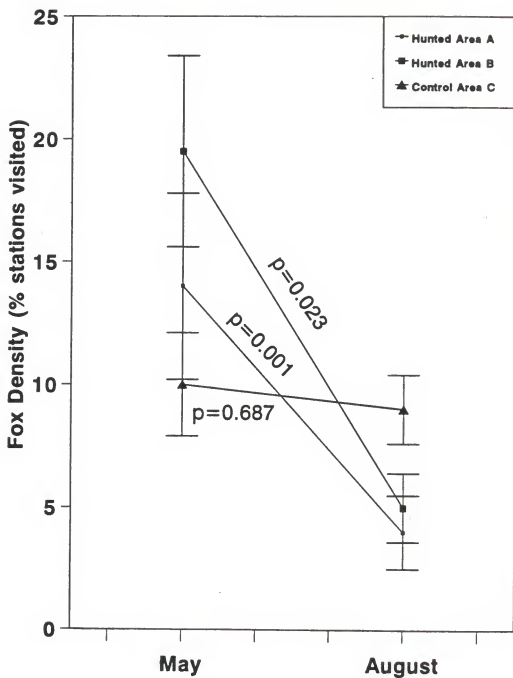


Figure 2-7. Culpeo fox relative densities before and after the 1989-hunting season in two hunted areas (A: $n = 3$ ranches: Catan Lil, L. Papay and L. Remolinos; B: $n = 2$ ranches: C. de los Pinos and Aquinco) and one unhunted area (C: $n = 2$ ranches: Collun Co and La Rinconada). Data are means ± 1 SD. Density comparisons were done with the Fisher randomization test. Data from Novaro (1991).

Mortality not caused by humans was low and did not appear to compensate for hunting mortality in the studied culpeo populations. Similarly, natural and hunting mortality were additive in a lynx population in Alberta (Brand and Keith, 1979). High natural mortality, particularly during years of low prey availability, may be a condition for making hunting mortality compensatory in lynx populations (Poole et al., 1994). Low natural mortality in the culpeo population, perhaps due to high prey availability (Chapter 4), may have precluded compensation between natural and hunting mortality.

Low culpeo mortality on C. de los Pinos in 1994 and 1995 also suggests that the assumption of similar prey productivity among sheep and cattle ranches is correct. Sheep were raised on C. de los Pinos for at least 8 decades until 1993, so if lower prey productivity affected culpeo survival on sheep ranches, the observed increase in this demographic rate in 1994 and 1995 to a level above survival on the control ranch should not be expected.

Fecundity rates

Density-dependent responses in fecundity could be important mechanisms for maintaining culpeo populations in

the mixed landscape of hunted and unhunted ranches.

Unfortunately, current data are not sufficient for examining these responses in detail.

The proportion of breeding females and litter size were similar on hunted and unhunted ranches. Both parameters were slightly higher on unhunted ranches, but this difference could be due to small sample sizes. Proportions of breeding culpeo females were similar to harvested coyotes (Gese et al., 1989) and lower than in lynx (Slough and Mowat, 1996).

Availability of resources to young lynx may determine their conception rate during fluctuations of their main prey (Brand et al., 1976; Knick, 1990). In a similar fashion, juvenile culpeos may be more likely to reproduce on hunted than unhunted ranches due to reduced population density resulting from hunting and higher availability of prey per individual. This density-dependent response could be facilitated by timing of the reproductive season, which immediately follows the hunting season. This mechanism may explain the presence of signs of ovulation and pregnancy in juvenile culpeos from hunted ranches.

Lack of reproduction of juvenile culpeos on the unhunted ranch was documented from a small number of radiocollared foxes and absence of signs of ovulation in the tracts of two females. Similarly, only one juvenile female was found pregnant on the hunted ranches. Therefore, no conclusive evidence is available for a density-dependent response of reproduction at an earlier age on hunted ranches, but the potential effect of this response on recruitment is low due to high juvenile mortality (Table 2-3).

Age structure and sex ratio

Based on data from age structure on hunted and unhunted areas, I cannot draw clear conclusions about differential fecundity or survival of pups and juveniles. The proportion of juveniles was ca. 40% on the control and on intensively hunted Catan Lil and La Papay ranches, but was higher than 55% on hunted C. de los Pinos and Remolinos ranches. These differences may be due to higher reproductive productivity and/or lower first-year survival on C. de los Pinos and Remolinos. Age distributions may reflect harvest pressure and recruitment in different populations when sampling bias by age is minimal or constant among populations (Robinson

and Redford, 1994). Sampling bias among culpeo age-structures was unlikely because methods of capture were similar on all ranches. However, interpretations of age distributions are limited due to the combined effects of fecundity and survival (Caughley, 1977).

The sex ratio of hunted culpeo populations in the study area has changed during the last 30 years. Crespo and de Carlo (1963) studied population characteristics of culpeos on Campo Grande ranch, ca. 10 km to the north of my study area (Fig. 2-1). They estimated a sex ratio significantly biased towards males (41% females), while data presented here show a ratio close to unity. A change of sex ratio in this direction, or even to one with more females than males, was documented for coyote populations subject to intense hunting (Knowlton, 1972; Berg and Chesness, 1978) and results in compensation for high mortality rates. The change in culpeo sex-ratio may be a consequence of increased hunting pressure during the late 1970s and 1980s, when fur prices peaked. If hunting pressure continues to decline in the 1990s, the sex ratio may reverse to one biased towards males.

Dispersal rates

Based on two aspects of the limited data available, dispersal of culpeos could be a mechanism to rebuild hunted culpeo populations. First, most, and perhaps all, culpeos that survived dispersed during their first or second year of life. Second, dispersal distances were large in relation to ranch size, and hunted and unhunted ranches are intermixed in the study area resulting in high connectivity (Taylor et al., 1993) between landscape elements with different hunting patterns. Thus the probability of dispersing culpeos reaching hunted areas is high.

Prediction 5 about dispersal direction was based on the assumption that culpeos were more likely to establish new ranges in areas of lower population density due to hunting. Insufficient data were available to test this prediction, but dispersal rate into hunted ranches appears to be larger than into unhunted ones.

The relationship between dispersal and population density on natal areas also may be significant in the regional dynamics of culpeos. I did not evaluate this relation because I expected sample sizes to be even smaller than for Prediction 5, due to high mortality on the hunted

ranch and because I was unable to tag a large number of pups. However, studies of the influence of population density on dispersal in other canids have found conflicting results. Harris (1981), MacDonald and Bacon (1982), and Trehwella et al. (1988) reported an inverse relation between density and dispersal distance for red foxes in Great Britain. Conversely, Allen and Sargeant (1993) found no effect of density on dispersal distance of red foxes in North Dakota. If the relation between density on natal areas and dispersal distance of culpeos was inverse, dispersal would play a limited role in regional population dynamics, because culpeos dispersing from un hunted ranches with high densities would be more likely to establish new ranges near their natal ones. Conversely, if culpeo density and dispersal distance were unrelated, dispersal would play a major role in rebuilding depleted populations over large areas (Allen and Sargeant, 1993).

Population trends in culpeo

Culpeo populations have been hunted in this area since the introduction of sheep at the beginning of the century (Crespo and de Carlo, 1963), and foxes probably sustained high hunting pressure for at least the last 30 years. Most

hunting is done by ranch workers who supplement their salaries with sales of fox fur (Novaro, 1995). Fur demand increased during the 1960s and 70s and pelt prices peaked at approximately U\$30 during the early 1980s. Pelt prices declined during the study from U\$15 in 1989 to U\$3 in 1993. Culpeo populations in the study area increased between 1989 and 1995 in spite of the continuing harvest. This population increase may therefore be a result of declining harvest pressure on hunted ranches.

Source-sink vs. intra-patch processes

Hunted populations of culpeos should decline and unhunted ones increase significantly every year according to the rates of increase calculated from survival and fecundity data. Thus, the dynamics of this culpeo population resemble a source-sink model, in which sink populations have negative rates of increase and source ones have positive rates (Hanski and Simberloff, 1996). However, Watkinson and Sutherland (1995) have argued that populations that would sustain themselves without immigration may appear to have negative rates of increase because the dispersal of individuals into them may depress fecundity or increase mortality through density dependence. According to

Watkinson and Sutherland (1995) the only ways to identify sinks and sources unequivocally are to determine the exact nature of density-dependent processes or to isolate sinks experimentally. Hanski and Simberloff (1996) added that the confounding effect of density dependence can be avoided by measuring rates of increase at low population density and in the absence of migration.

Migration occurred and culpeo population density was high (Appendix VII) in this study. Isolation of sinks was not feasible, as is the case in most field studies (Watkinson and Sutherland, 1995). A significant increase in natural mortality of hunted populations due to culpeo immigration was unlikely, because natural mortality was generally low, even after hunting mortality was removed in 1994. A density-dependent response in culpeo reproduction is not clear from this study. However, because of the timing of hunting and reproduction, and in spite of potentially high rates of dispersal of culpeos into hunted areas, culpeo densities on hunted ranches during the breeding season were depressed to about 30% of their pre-hunting level (Fig. 2-7). Thus dispersers are unlikely to reduce the availability of resources to breeding culpeos and

prevent a density-dependent response in reproduction. Furthermore, human-related mortality on hunted ranches is simply too high to maintain populations only from reproduction within a patch, regardless of any potential density-dependent response in reproduction.

The suggestions of Watkinson and Sutherland (1995) and Hanski and Simberloff (1996) about the effect of density dependence apply to populations not subject to hunting or perhaps with low levels of hunting by humans. High hunting mortality, however, overrides any potential density-dependent effect, and source-sink dynamics may occur if hunting is restricted to some landscape patches, leaving other patches of available habitat undisturbed, and if connectivity among patches is high.

This study shows that regional dynamics, likely through source-sink mechanisms, are essential for the persistence of hunted culpeo populations in northwestern Patagonia. If isolated, populations on hunted sheep ranches would near extinction within the life span of a culpeo. The culpeo harvest over the last 30 years may have been sustainable due to the maintenance of unhunted sources from which hunted populations have been rebuilt yearly. However, hunting

pressure is clearly not sustainable at the scale of individual hunted ranches, so in the absence of refugia on cattle ranches the whole population would undoubtedly collapse.

Management Implications

Hunting of culpeos is legal in all provinces of Patagonia except Tierra del Fuego. Monitoring of population trends was initiated only recently in other Provinces of Patagonia (Novaro and Funes, 1994), and no information is available on harvest levels for any area outside of southern Neuquén. There are no quotas or limits on harvest rates, except for Neuquén Province where a yearly bag-limit of 25 foxes per hunter was declared in 1992. However, enforcement capabilities are extremely limited throughout Patagonia (Novaro, 1993).

Under these limitations a harvest system regulated by spatial controls (McCullough, 1996; Joshi and Gadgil, 1991) is more likely to prevent overharvest than one that attempts to regulate size of harvest. Sustainable harvest by spatial control requires that a certain proportion and size of areas be kept as refugia in a mosaic of hunted and unhunted areas. This approach may fit well with the harvest pattern

described in this study for sheep and cattle ranches in southern Neuquén. Most of Patagonia has similar land-use practices to the ones in the study area, with the size of ranches varying according to primary productivity and land tenure. Harvest refugia could be designated on more inaccessible areas (particularly in the vicinity of sheep ranches to maintain connectivity) and on cattle ranches. Limited enforcement resources could be concentrated on enhancing culpeo productivity in these areas, for instance by controlling poaching and reducing populations of feral dogs.

However, two major difficulties arise when considering the spatial control approach. First, sink populations that occupy a large proportion of the habitat available in source-sink systems may contribute significantly to the regional population size and stability, e.g. through buffering of stochastic changes in population size (Howe et al., 1991). Therefore, management for sustainable use of culpeos should include protecting habitat quality on hunted areas, particularly considering that these are usually sheep ranches where overgrazing and habitat degradation are more prevalent. Improved habitat quality would also increase the

availability of prey (Chapter 4), thus reducing culpeo predation on sheep. Second, the proportion of unhunted patches in this mosaic could decline to a level that would make regional populations of culpeos collapse. The mosaic of sheep and cattle ranches is a dynamic one, with landowners periodically changing land-use practices due to changes in wool and meat prices. Simulation models are needed to predict the threshold level in the proportion of hunted and unhunted areas for different patch sizes where the collapse would occur (Chapter 3). Because of the two problems described above, and the continued degradation of habitat in Patagonia as a result of overgrazing, I believe that sustainable use of culpeos may be achieved only if local wildlife agencies and resource users manage culpeo populations on hunted ranches simultaneously with the implementation of a spatial control strategy.

CHAPTER 3
CULPEO POPULATION DYNAMICS: HOW MANY SOURCES
ARE NECESSARY FOR A SUSTAINABLE HARVEST?

Introduction

Modeling tools can show which key ecological processes determine the decline or increase of biological populations and reveal the consequences of different management options. The use of population simulation models in conservation biology has increased dramatically in recent years (Hamilton and Moller, 1995). Because landscape complexity can have a significant impact on the dynamics of biological populations (Hanski and Gilpin, 1996), recent developments of simulation models have incorporated a spatial component to simulate that complexity (Akçakaya et al., 1995).

In a study of the impact of hunting on culpeo foxes (Pseudalopex culpaeus) in northwestern Patagonia, Argentina, I concluded that their population dynamics are strongly influenced by the spatial distribution of hunting (Chapter 2). However, the following unanswered questions emerged from that study. First, what are the consequences of

modifying the demographic parameters of that culpeo population through management? If managers wanted to increase or decrease the size of the culpeo population, for example, they would need to know which changes of parameters would be most effective. Second, what are the consequences of potential biases in the estimation of demographic parameters? All vital rates were estimated using small sample sizes, so it is important to know how the predictions about population dynamics of culpeos would be affected by errors in those rates. Third, the mosaic of hunted and unhunted ranches that allows this population to sustain high harvest levels is dynamic and could change dramatically due to external factors. The decision by land owners to raise sheep (and promote culpeo hunting) or cattle (and ban culpeo hunting) is based on constantly changing market prices of wool and beef, as well as on other factors including primary productivity (see Chapter 1, Introduction). Thus the last, and perhaps most important, question about culpeo conservation in the area is: What are the consequences of changes in the proportion of hunted and unhunted areas on the sustainable harvest of culpeos? The purpose of this

part of my study was to attempt to answer these questions using population simulation models.

Methods

I studied the population dynamics of culpeo foxes using the RAMAS/metapop computer simulation model (Akçakaya, 1994). The RAMAS/metapop model had spatial structure defined by the geographic location of populations, migration among populations, and correlation among their vital rates. I incorporated stage structure of each population and demographic and environmental stochasticity into the model. I validated the model by comparing output population trends during the first eight years with population trends estimated with the scent-station method between 1989 and 1995 (Chapter 2).

In simulation studies applied to conservation the result of interest is usually the risk of population decline or extinction during a certain period (Burgman et al., 1993; McCarthy et al., 1995). However, culpeo populations in Patagonia are managed as both a pest (because they prey on sheep; Bellati and von Thungen, 1990) and a resource (due to the value of their fur; Novaro, 1995), so it was necessary to evaluate simultaneously the risks of population increase

and decline. Thus I used the percent change in population size as the dependent state variable in the model.

Model Building

To simulate the dynamics of a population on a continuous landscape, I modeled the culpeo populations of the six hunted and unhunted ranches studied (Collun Co, La Rinconada, C. De los Pinos, Catan Lil, La Papay, and Los Remolinos) and of six additional ranches located within the perimeter defined by the former six (Figures 3-1 and 2-1). For the additional ranches I collected information on their size and hunting pattern (hunted or unhunted for culpeos). Ranch size and hunting pattern are indicated in Table 3-1. Total area of the 12 ranches was 2,690 km², with 33% on unhunted cattle ranches. This percentage was similar to the percentage of area on cattle ranches when only the six intensively studied ranches were considered (34%).

I used as input data for the RAMAS model the demographic parameters and densities of culpeos estimated on hunted and unhunted ranches through the analysis of carcasses, radiotelemetry, and scent-station indices between 1989 and 1996 (Chapter 2 and Appendix VII). Initial culpeo

abundance on the six ranches studied was calculated using the equation

$$N = (SSI / B) * A,$$

where SSI = 1989 scent-station index, B = slope of the regression equation between SSI and culpeo density (0.358, Appendix VII), and A = ranch size (km²). Initial age structures were calculated using proportions of culpeos captured on each ranch (Table 3-1). I assumed age structures did not change during the study. Initial abundances and age structures on the additional six ranches were calculated using average culpeo densities and age structures on the six hunted and unhunted ranches and ranch size (Table 3-1).

I modeled all individuals in the population (females and males, sex ratio 1:1) and used a matrix model with three stages (juveniles, one-year-olds, and two-year-olds and older). Two adult age classes were considered because survival rates of one-year-old adults were slightly lower than of older culpeos, and because some one-year-old culpeos dispersed (Chapter 2).

Vital rates were calculated following methods proposed by Caswell (1989) and Akcakaya (1994). Reproductive data

Table 3-1. Initial population structure of culpeos, hunting pattern, and area of 12 ranches used in the simulation of culpeo population dynamics with RAMAS/Metapop. Initial population structure is represented by the number of individuals in the juvenile (Ni_0), one-year-old (Ni_1), and two-year old and older (Ni_2) age classes, respectively. Under H I indicated if there was culpeo hunting (yes) or not (no). Area of each ranch is given in km^2 . Some small neighboring ranches with similar hunting patterns were grouped; the name used was that of the largest ranch.

Ranch	Ni_0	Ni_1	Ni_2	H	A
Collun Co ¹	36	22	91	no	400
Rinconada ²	5	3	12	no	80
C. Pinos ¹	41	23	65	yes	180
Remolinos ¹	29	17	46	yes	230
La Papay ¹	58	33	91	yes	280
Catan Lil ¹	17	9	26	yes	250
Palitue ³	15	9	37	no	200
S. Ignacio ³ (ranch)	16	10	41	no	220
Chacayal ⁴	24	13	37	yes	150
Sihuen ⁴	32	18	37	yes	200
Malleo ⁴	40	22	62	yes	250
S. Ignacio ⁴ (reservation)	40	22	62	yes	250
Total					2,690

¹ Initial age structure was calculated using 1989 density-estimates, ranch size, and age structure of culpeos captured during the study on each ranch.

² Initial age structure was calculated using 1989 density-estimate, ranch size, and age structure of culpeos on Collun Co.

Table 3-1---continued.

³ Initial age structure was calculated using ranch size and extrapolating average 1989-culpeo-density from Collun Co and La Rinconada and age structure from Collun Co.

⁴ Initial age structure was calculated using ranch size and extrapolating average 1989-culpeo-density and age structure from C. Pinos, Remolinos, La Papay, and C. Lil.

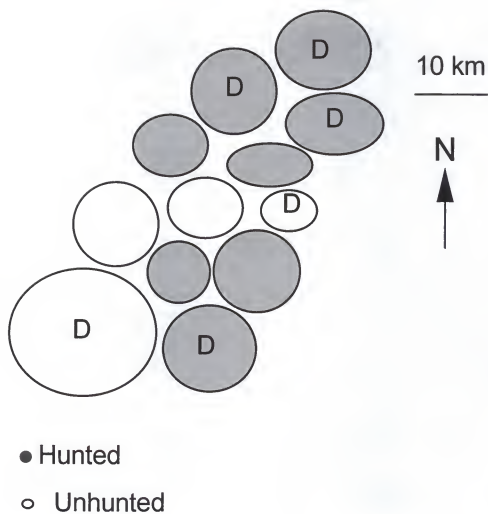


Figure 3-1. Twelve sheep (hunted) and cattle (unhunted) ranches in northwest Patagonia. D: corresponds to ranches where demographic data were collected.

were analyzed as maternity rates and the transition matrix was constructed assuming age-structure data were from a pre-breeding census. This was considered reasonable because the hunting season (when most carcasses were collected) is during the winter months and the birth pulse (Caswell, 1989) of culpeos occurs during the spring and early summer. I used the vital rates estimated on unhunted Collun-Co ranch (Chapter 2) to build the transition matrix

0.00	1.07	1.07
0.70	0.00	0.00
0.00	0.76	0.76,

which was used for all unhunted ranches. The transition matrix for hunted ranches was estimated with survival data from C. de los Pinos ranch and fecundity data from all hunted ranches (Chapter 2):

0.00	0.11	0.11
0.64	0.00	0.00
0.00	0.70	0.70

This matrix was assigned to hunted ranches using the catastrophe feature of RAMAS/metapop, with a local catastrophe probability of 1.0 (Akçakaya, 1994).

Fecundity rates on hunted ranches were calculated averaging litter-size estimates obtained during my study (3.6 pups/female, $SD = 1.3$, Chapter 2) with Crespo and de Carlo's (1963) estimate (5.2 pups/female, $SD = 1.9$). Preliminary simulations using my estimate of litter size produced population trends that did not increase during the first eight years as shown by scent-station results (Chapter 2). Simulations using a combination of both estimates produced trends similar to scent-station results.

I did not include density dependence in the simulations. Culpeo populations on hunted ranches have exponential rates of increase < 0 (based on schedules of fecundity and survivorship, Chapter 2) probably due to the "systemic" pressure (Shaffer, 1981) of hunting. Including density dependence when populations are subject to such pressures could lead to underestimation of extinction risks (Akçakaya, 1994; Ginzburg et al., 1990). Furthermore, almost no information is available on density-dependent mechanisms in culpeo populations (Chapter 2).

However, density dependent effects on vital rates likely occur in this culpeo population, particularly if regional densities continue to increase, perhaps due to

lowering hunting pressure (Chapter 2). To avoid underestimating the long-term effects of density-dependent mechanisms, I decided to run the simulations for only 8 years and use 1989 densities to calculate initial abundances. Demographic parameters were obtained during seven years (between 1989 and 1996, Chapter 2), so I assumed that the effects of density dependence at current densities were incorporated into vital rates estimated from those parameters. Culpeo density increased on two unhunted ranches and did not change significantly on four hunted ranches between 1989 and 1995. Therefore, I assumed that density dependent effects would not change significantly during 8-year simulations.

Dispersal rates of juvenile, one-year-old, and older culpeos were 83, 20, and 0%, respectively, based on proportions of radiocollared culpeos that dispersed (Chapter 2). Migration rates among ranches were calculated assuming a monotonically declining rate of dispersal with distance (Wolfenbarger, 1946; Kitching, 1971; Akcakaya, 1994), which was reasonable based on available data on culpeo dispersal distances (Chapter 2). The migration rate between ranches i th and j th was

$$m_{ij} = 5.8 * \exp [(-D_{ij}^{0.22}) / 0.58] \quad \text{if } D < 90 \text{ km}$$

$$0 \quad \text{if } D > 90 \text{ km}$$

where D_{ij} was the distance between the geographic center of the two ranches. Maximum dispersal distance was that recorded in the radiotelemetry study, although culpeos may disperse larger distances occasionally (W. Johnson, pers. comm.).

Environmental stochasticity was simulated by making RAMAS choose vital rates at random from a normal distribution with means taken from each transition matrix and standard deviations from the matrix

0.00	0.05	0.05
0.20	0.00	0.00
0.00	0.18	0.18

These standard deviations were calculated from annual variation of vital rates on Collun Co and C. de los Pinos ranches (Chapter 2). Demographic stochasticity was also included in the model, because it could have a significant effect if culpeo abundance was reduced to a small number of individuals, which was likely on small ranches. One thousand replications were used in each simulation.

The RAMAS/metapop model predicted population trends that were similar to the seven-year population trend recorded in the field using scent-stations (Figure 3-2 and Chapter 2). The simulated population increased in size by 65% in 8 years from an initial estimate of 1144 culpeos in 1989, while according to scent-station results the culpeo population increased by 80% during the same period.

Sensitivity analysis

The effects on culpeo-population dynamics of modifying demographic rates through management and of biases in the estimation of those rates were analyzed using sensitivity analysis (Burgman et al., 1993). Sensitivity of the model was measured by varying parameters by 10, 20, and 30% around their estimated value and measuring the change in population trend after 8 years of simulation. This change was used as an index of the sensitivity of the culpeo model to each parameter.

I studied model sensitivity to survival, fecundity, and migration rates. Increases in survival rates of 20-30% produced population increases that were unrealistically high, assuming the population would be regulated by density-dependent effects at high densities. However, these results

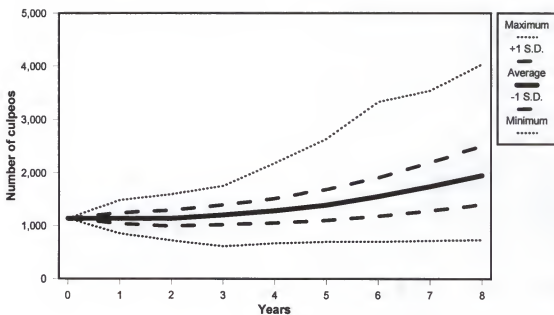


Figure 3-2. Predicted population trend of culpeos using demographic data from field study and RAMAS/metapop simulation model, with 1,000 simulations.

were considered useful for comparison between relative effects of the three parameters.

Migration is likely to have strong demographic effects on hunted culpeo populations that appear to be rebuilt annually by immigrants from unhunted areas (Chapter 2). Thus I also evaluated sensitivity of the population trend on one of the hunted ranches (C. De los Pinos) to changes in migration.

Changing landscape

The implications of changes in the proportion of hunted and unhunted areas were analyzed by simulating variations in the proportion between cattle and sheep ranches. I increased the size of the study area to include a larger number of ranches. This was done to simulate a more continuous change of proportions between ranch types than if only 12 ranches were considered. The size of the study area was doubled (to 5,236 km²) by including 11 additional ranches for which I recorded size, land use, and culpeo-hunting pattern (Table 3-2 and Figure 3-3). This area encompassed approximately 1/3 of southern Neuquén Province, and 37% was on unhunted cattle ranches. To study the effect of a declining proportion of unhunted areas, I switched

Table 3-2. Initial population structure of culpeos, hunting pattern, and area of 11 additional ranches used in the simulation of culpeo population dynamics in southern Neuquén with RAMAS/Metapop. Initial population structure is represented by the number of individuals in the juvenile (N_{i_0}), one-year-old (N_{i_1}), and two-year old and older (N_{i_2}) age classes, respectively. Under H I indicated if there was culpeo hunting (yes) or not (no). Area of each ranch is given in km^2 . Some small neighboring ranches with similar hunting patterns were grouped; the name used was that of the largest ranch.

Ranch	N_{i_0}	N_{i_1}	N_{i_2}	H	A
Pilolil (ranch) ¹	10	6	24	no	130
Chapelco ¹	7	5	19	no	100
Quemquemtreu ¹	37	23	93	no	500
Collon Cura ¹	22	14	56	no	300
Pilolil (public) ²	40	22	62	yes	250
Sanico ²	32	18	49	yes	200
Franco ²	5	3	7	yes	30
Aquinco ²	14	8	21	yes	86
Caleufu ²	32	18	49	yes	200
Banadera ²	24	13	37	yes	150
Alicura ²	95	53	148	yes	600
Total					2,546

¹ Initial age structure was calculated using ranch size and extrapolating average 1989-culpeo-density from Collun Co and La Rinconada and age structure from Collun Co.

² Initial age structure was calculated using ranch size and extrapolating average 1989-culpeo-density and age structure from C. Pinos, Remolinos, La Papay, and C. Lil.

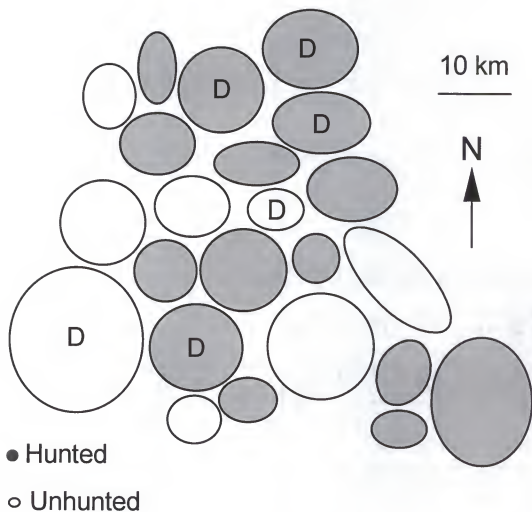


Figure 3-3. Twenty-three sheep (hunted) and cattle (unhunted) ranches in northwestern Patagonia. D: corresponds to ranches where demographic data were collected.

unhunted to hunted ranches one at a time and ran the model with the remaining variables and parameters unchanged. I evaluated the results by measuring change in population size after 8 years of simulation.

Finally, a combination of changes in the landscape and vital rates was evaluated. Survival is the vital rate that could be affected most directly through management by changing hunting pressure. A decline of culpeo survival occurring simultaneously with a decrease in the proportion of unhunted areas could have a compounded effect on culpeo population dynamics. Therefore I evaluated the effect of decreasing the proportion of unhunted ranches from the current level with survival rates that were 3, 6, and 10% lower than estimated rates.

Results

Sensitivity Analysis

Adult survival was the vital rate to which the culpeo model was most sensitive (Figures 3-4 and 3-5). Juvenile survival had the same effect as fecundity, because these rates were multiplied when constructing the Leslie matrix. A 10% decline in fecundity and adult survival led to population sizes in the eighth year of simulation that were

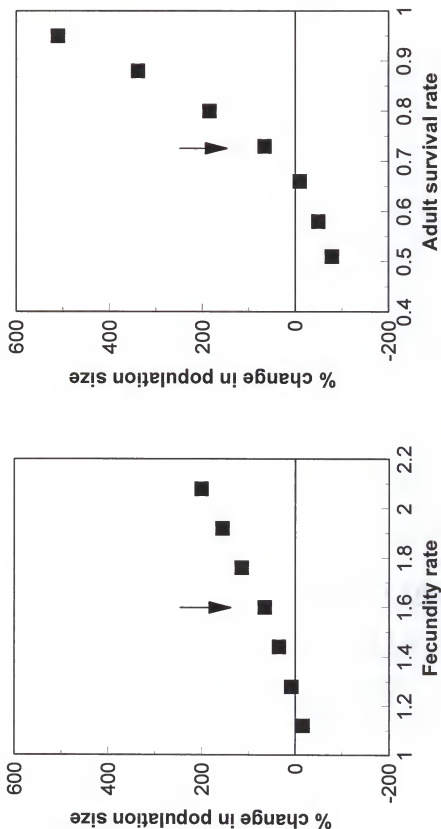


Figure 3-4. Sensitivity analysis of changes in culpeo population size after 8 years of simulation in relation to changes in fecundity and survival. Arrows indicate current estimates. Values to the left and right correspond to rates that are 10, 20, and 30% smaller and larger than current rates, respectively.

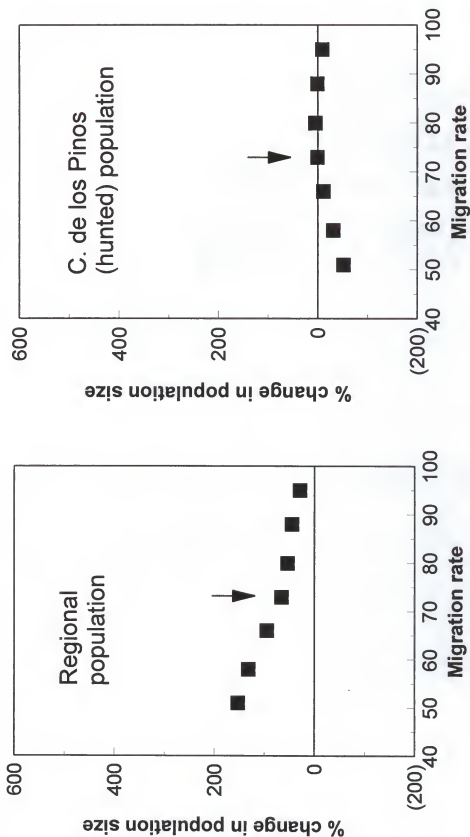


Figure 3-5. Sensitivity analysis of changes in culpeo population size after 8 years of simulation in relation to changes in migration rates. Arrows indicate current estimates. Values to the left and right correspond to rates that are 10, 20, and 30% smaller and larger than current rates, respectively.

19 and 45% lower, respectively, than the size predicted with current rates (Figure 3-4). The 10% reduction in adult survival (from 0.73 to 0.66) produced a 20% decline from the initial population size.

The effects of migration rate on total (regional) population size and population size on hunted ranches were reversed (Figure 3-5). A 20% decline in overall migration rates produced an 8th-year total population size that was 40% larger than with current rates, and a population size on C. de los Pinos that was 30% smaller (Figure 3-5). The increase in total population size with lower migration was due to marked increases of population sizes on unhunted ranches. Higher migration rates than the estimated rate resulted in reductions of regional population size.

Changing Landscape

Culpeo populations collapsed under current hunting pressure when the percentage of area on unhunted ranches fell below 30% (Figure 3-6). A 7% decline in this percentage (from the current one of 37%) would occur if cattle were replaced by sheep on three small to medium-sized ranches (like Rinconada, Chapelco, and Pilolil), or on only one large ranch (like Collun Co, Tables 3-1 and 3-2).

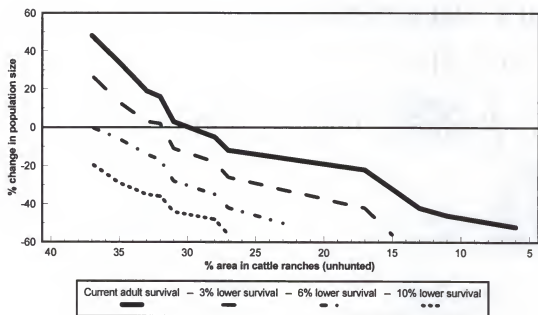


Figure 3-6. Change in population size of culpeos after 8 years of simulation in relation to changes in the percentage of area in cattle ranches. The relationship is presented for current adult survival and for 3, 6, and 10% lower adult survival.

Population collapse as a result of a reduction in total unhunted area was more likely when only a small decline in adult survival was added. When adult survival was reduced by 3%, the culpeo population declined with any reduction in the percentage of unhunted area larger than 5% (Figure 3-6). A 5% reduction would occur if cattle were replaced by sheep on only one small and one medium-sized ranch. When culpeo adult survival was reduced by 6%, any reduction in unhunted area resulted in a decline of culpeo abundance. Finally, if adult survival declined more than 6%, even the current percentage of unhunted area would lead to declining populations (Figure 3-6).

Discussion and Management Implications

Adult survival had the strongest effect on population trends of culpeos among the vital rates studied, and it also affected markedly the proportion of unhunted area required to maintain a stable population. Fecundity had a smaller effect than adult survival on the population size predicted with the model due to the low juvenile survival. Most of the non-migrating juveniles born on hunted ranches and juvenile immigrants into those ranches died during their first year of life. Migration rate had an even smaller

effect than fecundity on total population size, and in the opposite direction than adult survival and fecundity.

Higher migration rates produced smaller population sizes than the estimated migration rate. When more culpeos leave unhunted ranches, their contribution to the regional population size is reduced due to high mortality on hunted ranches. However, population size on hunted ranches increased with increasing migration rates, at least between 50 and 80%. Migration rates >80% did not result in larger population sizes on hunted ranches, perhaps due to depletion of source populations on unhunted ranches. Thus it appears that lower migration than that observed in the field study would lead to a more heterogeneous spatial-distribution of culpeos (with higher densities on unhunted ranches and lower densities on hunted ones), and higher migration would result in a more homogeneous distribution. The importance of small levels of migration in maintaining declining populations also has been documented for puma (Puma concolor) by combining field data and simulation techniques (Beier, 1993).

A relatively small reduction in the proportion of area on unhunted ranches would result in declining culpeo

populations. According to the simulation results, the threshold in the proportion of unhunted to hunted area between increasing and declining populations is approximately 30%. However, the interaction between the proportion of unhunted to hunted area and adult-survival rate of culpeos is strong, so this threshold could change significantly if hunting pressure changed.

During the field study of culpeo demography (Chapter 2), fecundity, survival, and migration rates were estimated using small sample sizes, so biases of their means and standard deviations were likely. According to the results of the sensitivity analysis, research efforts should concentrate on estimating survival rates of adult culpeos accurately. Biases in fecundity, juvenile survival, and migration rate estimates would have a smaller influence on the predictions of culpeo population trends.

Density-dependent effects on vital rates also need to be investigated. Inverse density-dependence in reproduction was reported for small puma populations (Padley, 1990), and it may be significant for heavily hunted culpeo populations. However, high migration between ranches may prevent culpeos from reaching densities low enough to experience this type

of density dependence. On the other hand, high densities on unhunted ranches may be common, so it is necessary to evaluate density dependent effects on fecundity, survival, and dispersal in those areas.

A better understanding of density dependent mechanisms in culpeo populations would allow researchers and managers to conduct longer-term simulation studies. The main constraint on extending the simulation beyond 8 years in this study was the uncertainty about density dependence when culpeo populations reached densities much higher or lower than current levels.

Another aspect that needs further study is the demographic significance of populations on hunted sheep ranches. Sink populations (Chapter 2; Pulliam, 1988) that occupy a large proportion of the habitat available may contribute significantly to the regional population size and stability (Howe et al., 1991). However, culpeo habitat on sheep ranches may be deteriorating due to the effect of overgrazing and desertification. The culpeo model developed in this study would allow an evaluation of the effect of reduced carrying capacity on hunted ranches to regional

population stability. A better understanding of density dependent mechanisms is necessary to model this effect.

For management purposes, the main variable to monitor in this system is the proportion of area on cattle and sheep ranches. Management agencies in the region have very limited resources to regulate the harvest of culpeos on sheep ranches. Sustainability in the harvest of the culpeo population could be achieved more likely by a spatial-control strategy (McCullough, 1996; Joshi and Gadgil, 1991). Spatial control requires that a certain proportion and size of areas are kept as refugia in a mosaic of hunted and unhunted areas. This strategy may fit well the processes described in the population dynamics of culpeos (Chapter 2 and this study) on sheep and cattle ranches in southern Neuquén.

However, the mosaic of hunted and unhunted areas is dynamic, and the amount of area on cattle ranches could fall below the threshold of culpeo-population stability if only a small number of cattle ranches switched to sheep raising. During the field study two ranches switched from sheep to cattle raising due to plummeting wool prices in the early 1990s. So the recent changes in the area were in the

direction of a more sustainable harvest of culpeo populations. If wool prices increase or if beef prices decline, this trend could reverse quickly. Management agencies should devise a strategy to maintain some source culpeo populations that are independent of land use, perhaps by limiting hunting on more rugged and inaccessible areas. These permanent sources should be located primarily in areas with higher concentration of or larger sheep ranches, to maintain connectivity between hunted and unhunted landscape patches. And perhaps most importantly, the role of existing refugia on cattle ranches could be enhanced by limiting culpeo adult mortality due to feral dogs and poachers. This strategy would require a minimal investment by management agencies. Cattle ranchers would be supportive of these measures (because they want high culpeo densities to help control hare abundance, Chapter 4) and could implement the measures themselves with technical guidance from management agencies.

CHAPTER 4
A NATIVE CARNIVORE ASSEMBLAGE RELYING ON INTRODUCED PREY
IN NORTHWEST PATAGONIA

Introduction

Many carnivores prey intensively on introduced species if these are more readily available or vulnerable (Pyke et al., 1977) than native species. This dietary shift has been reported for coyotes (Canis latrans) in many areas of North America (Andelt, 1985; MacCracken and Hansen, 1987), dingoes (Canis familiaris dingo; Corbett, 1995) and red foxes (Vulpes vulpes; Newsome et al., 1989; Pech et al., 1992) in Australia, and pumas (Puma concolor) in Florida (Maehr et al., 1990). However, no studies to date have reported on an entire carnivore assemblage consuming primarily introduced prey.

The geographical ranges and densities of many native species in southern South America have been greatly reduced due to hunting and habitat degradation (Roig, 1989). Guanacos (Lama guanicoe) and lesser rheas (Pterocnemia pennata) were once the dominant species in the Patagonia

region of South America (Redford and Eisenberg, 1992).

Domestic livestock (sheep, Ovis aries, cattle, Bos taurus, and horses, Equus caballus) was introduced since the early 1500s and severely altered the vegetation of the pampas and steppe (Darwin, 1962). Game species (primarily European hare, Lepus europaeus, European rabbit, Oryctolagus cuniculus, and red deer, Cervus elaphus) were introduced into Patagonia during the late 1800s and early 1900s (Grigera and Rapoport, 1983; Funes, 1996), reaching high densities and accelerating habitat destruction (Ramirez et al., 1981; Veblen et al., 1992). Hares have colonized most of Argentina and part of Chile. In Argentina the ranges of rabbits and red deer are restricted to parts of Patagonia but continue to expand, perhaps due to ongoing habitat disturbance by humans (Funes, 1996). Thus, changes in the prey base for carnivores have operated over most of the land area of terrestrial ecosystems in the region. These changes could have significant ecological and conservation implications for those ecosystems and particularly for populations of native predators and the remaining native prey (Estes, 1996; Simonetti, 1988).

The food habits of some of the terrestrial carnivores in southern South America have been extensively studied in protected areas, where the prey base is relatively undisturbed (Iriarte et al., 1991; Johnson and Franklin, 1994a; Branch et al., 1996; Meserve et al., 1996; earlier studies reviewed by Medel and Jaksic, 1988). Few studies on carnivore food habits have been conducted outside of protected areas (Crespo, 1975; Yanez et al., 1986).

None of the studies on carnivore food habits outside of protected areas have reported information on current prey availability, which is necessary to understand prey selection patterns. Even most studies in protected areas have concentrated on a small range of potential prey, mainly small mammals, with the exception of Iriarte et al. (1989, 1991) and Johnson and Franklin (1994a) in Torres del Paine National Park.

The most abundant terrestrial carnivore species in Patagonia are the culpeo fox (Pseudalopex culpaeus), the South American gray fox or chilla (P. griseus), and common and Patagonian hog-nosed skunks (Conepatus chinga and C. humboldtii, respectively; Crespo and de Carlo, 1963; Johnson et al., 1990). Other carnivore species are the puma,

Geoffroy's cat (Oncifelis geoffroyi), pampas cat (O. colocolo), lesser grison (Galictis cuja), and Patagonian weasel (Lyncodon patagonicus) (Redford and Eisenberg, 1992).

The purpose of this study was to describe the food habits and prey selection of predators on rangelands in northwest Patagonia, Argentina, and particularly to evaluate the role of introduced herbivores as prey. The study was conducted between May of 1989 and November of 1994, as part of an assessment of the impact of hunting on culpeo foxes, so most of the information presented refers to this species. Data on chilla foxes, pumas, common hog-nosed skunks, and Geoffroy's cats were obtained opportunistically during the study and used to describe the food habits of other dominant species of the carnivore assemblage in the region. I described diet and prey availability for most carnivores as relative biomass to evaluate the energetic contribution of each item, and analyzed prey selection by comparing relative biomass available and consumed. For culpeos I also analyzed annual and seasonal patterns of prey selection, which may have a significant effect on native and domestic prey due to fluctuations of the European hare, the culpeo main prey (Crespo and de Carlo, 1963; Novaro et al., 1992).

Materials and Methods

Study Area

The study area was located on six ranches in northwestern Patagonia, Province of Neuquén, Argentina. Ranches were chosen to represent dominant land-use types in the region. Cattle raising is the main activity at Collun Co ranch, sheep raising predominates at Catan Lil, La Papay, and Cerro de los Pinos ranches, and cattle and sheep are raised at La Rinconada and Los Remolinos ranches. The total area of all six ranches was 1,420 km². The region falls within the Patagonian Phytogeographic Province, Occidental District (Cabrera, 1976). The vegetation is characterized by a mixed steppe of grass and shrubs. Dominant species were Mullinum spinosum, Senecio sp., Stipa sp., and Poa sp.

The weather is dry and cold, with frosts throughout the year and frequent snowfalls in winter. Mean, mean highest, and lowest annual temperatures were 11, 17.4, and 2.5°C, respectively. Mean annual rainfall ranged from 28 cm to 75 cm at different ranches, and was primarily concentrated during the winter.

Topographically the study sites consisted of great plains 800 to 900 m high, dissected by steep, rugged canyons

and valleys. In the bottom of the valleys there were humid areas with dense herbaceous vegetation, called "mallines," where the dominant species were Cortadeira araucana, Juncus sp., and Carex sp. These areas have a high primary productivity (Movia et al., 1982).

Food Habits

I determined food habits of carnivores through the analysis of stomach contents and feces. Stomachs were obtained from carcasses of animals killed by hunters between April 1989 and November 1994. Most animals were killed during the fall and winter seasons (April 15 through September 15), when hunting for fur takes place. I also collected carcasses of culpeos killed for predator-control purposes during the spring of 1993 and summer of 1994. To supplement the information on seasonal changes in culpeo diet, I collected culpeo feces between January of 1993 and November of 1994. Puma and Geoffroy's cat feces were also collected opportunistically during 1993 and 1994. I followed the criteria given by Iriarte et al. (1991) and Johnson and Franklin (1991, 1994a) to identify feces of pumas, Geoffroy's cats, and culpeos, respectively, and to distinguish them from those of other carnivores.

Furthermore, culpeo feces were collected only in areas where chillas do not occur.

Three hundred and twenty culpeo, 42 chilla, 25 skunk, four puma, and three Geoffroy's cat stomachs were collected and analyzed between 1989 and 1994. Additionally, 335 culpeo, 70 puma, and 7 Geoffroy's cat feces were collected and analyzed during 1993 and 1994.

I recorded age and sex of the animal for stomachs and approximate age of fecal samples. Stomachs were preserved in a 10%-formalin solution and feces were air dried. Analytical techniques followed procedures described by Korschgen (1980). Prey items were identified to the species level whenever possible. Volume and mass of prey items in stomachs were measured to the nearest ml and g, respectively. For the identification of mammalian prey, bones and teeth were compared to specimens in the collection of the Florida Museum of Natural History, University of Florida, and to photographs provided by Pearson (1995). Casts of hairs were made on stencil corrector fluid (Korschgen, 1980), and their medulla and scale patterns were compared to keys based on those characters for the mammals occurring in the study area (Chehebar and Martin, 1989;

Capurro et al., unpubl. data.)). Prey items were identified as carrion if they were too large to have been killed by the carnivore (eg. cattle, horse, or red deer for culpeos; all ungulates for chillas; and ungulates and adult European hare for skunks) or when they contained larvae of Diptera. Thus, the estimated consumption of biomass may be an underestimate because I may have not detected Diptera larvae in all cases (e.g., some culpeo prey identified as sheep may have been consumed as carrion). Birds were identified to species level only when remains other than feathers were found. Lizards were identified to generic level by herpetologists at the Museo de Historia Natural B. Rivadavia (Buenos Aires), and arthropods were identified to ordinal level.

I present results as percent occurrence (number of times an item occurred as percentage of the total number of prey items in all stomachs or feces) and as percent mass of each item for stomach contents. Most samples obtained for pumas and Geoffroy's cats were feces. Small and large prey have differential digestibility and the number of field-collectable feces can be inversely related to prey size (Ackerman et al., 1984; Weaver, 1993). I calculated the relative biomass and numbers of prey consumed by pumas using

a regression equation given by Ackerman et al. (1984). No equation is available for Geoffroy's cats, so data are presented as percent occurrence in feces.

Prey Availability

Data on prey availability were obtained to provide an evaluation of the relative biomass of introduced (domestic and wild) and native prey in the study area. Data on food habits, mainly from stomach contents, were gathered during six years from a large area (ca. 1,400 km²). However, it was not feasible to collect data on abundance of all prey available at comparable temporal and spatial scales, except for domestic species. Thus, I obtained estimates of density of the main wild species and their carrion during fall and winter seasons on sites that were representative of dominant habitat types and extrapolated density estimates to the entire area. Some of these estimates were obtained from field evaluations in this study and some from surveys conducted in the same area between 1982 and 1988 (and in 1995 and 1996 for carrion) by personnel of the local wildlife agency. I interviewed ranch owners and workers repeatedly during the study to detect significant changes in abundance of wild large-body-sized species (exotic and

native). I evaluated potential changes in relative densities of other species (hares, small mammals, and edentates) by repeating surveys every fall-winter season between 1989 and 1994. Estimates of density during spring and summer were obtained only for the European hare, the primary prey of culpeos (Crespo and de Carlo, 1963; Novaro, 1991). Body-mass estimates were used to assess biomass of different prey.

Introduced domestic species. The densities of sheep, cattle, and horses on each ranch were calculated using total counts and body masses provided by landowners between 1989 and 1994 and the size of the ranches. Standard deviations in densities were obtained averaging data among ranches and years. Densities of adults, yearlings, and juveniles were multiplied by average body mass of each age class to estimate the total biomass of each species.

Introduced wild species. Densities of European hares and red deer were estimated on one sheep and one cattle ranch using night transect counts. Line transects (Buckland et al., 1993) were conducted along four secondary roads and trails: one 14.1-km-long transect in Cerro de los Pinos, and three transects (7.3, 17.8, and 21.2-km long, respectively)

in Collun Co ranch. Each transect was sampled three to four times during late fall and early winter (May through July) between 1991 and 1994 to estimate annual trends in density. Numbers of red deer sightings in 1991 and 1992 ($n = 6$) were too small to estimate densities. Numbers of sightings during fall and winter of 1993 and 1994 were 39 and 32, respectively, and no differences were detected between density estimates ($P > 0.25$), so estimates from both years were averaged. To obtain seasonal estimates of hare density all transects were sampled also two to four times each during the spring of 1993 and summer of 1994. The number of sightings of deer during spring and summer were not large enough to estimate densities. All transects covered the main three habitat types: valleys, steppes, and slopes. Data were analyzed using program DISTANCE (Laake et al., 1993). Results are presented as mean density ± 1 SE.

To assess hare densities in the entire study area, relative densities were estimated on all ranches during late fall and winter between 1989 and 1994 using the pellet-count method (Novaro et al., 1992). Hare densities in ranches where transect counts were not conducted were calculated by calibrating (Lancia et al., 1994) pellet count results with

density estimates from transect data for Cerro de los Pinos and Collun Co ranches. I did a linear regression analysis (Sokal and Rohlf, 1995) between the square root of the number of new pellets produced / day-sampling unit and the density of hares estimated each winter in each ranch ($n = 8$). I used a resampling regression (program Resampling-Stats, Bruce et al., 1995) due to lack of independence among observations (Edgington, 1995). Average body mass of hares was estimated using proportions in each age class and body masses estimated in a site ca. 100 km away from the study (Amaya, 1984; Bonino and Bustos, 1994; Brandani et al., 1982). Deer body mass was obtained from kill data collected by the local wildlife agency (A. del Valle, pers. comm.).

Native species. Density estimates of guanacos (Lama guanicoe), lesser rheas (Pterocnemia pennata), and passerine birds during the fall and winter seasons were obtained from previous studies (Gader et al., 1987; del Valle, 1982; Travaini et al., 1989). Interviewed ranch owners and workers indicated that guanaco and rhea densities did not change significantly between 1989 and 1994. I conducted diurnal line-transect counts of guanacos and rheas along trails in all six ranches during the fall and winter of 1989

to 1994 and the summer of 1994. Numbers of sightings were insufficient to estimate densities using standard transect methods (Buckland et al., 1993), so I used these data only to evaluate temporal trends. Transect lengths were 9.0 km in Cerro de los Pinos, 8.5 km in Collun Co, 13.4 km in La Rinconada, 7.3 km in Catan Lil, 22.3 km in Los Remolinos, and 21.9 km in La Papay. All transects were driven four times each season at a speed of 5-10 km/hr. No information was available on annual trends in passerine-bird density. Body masses of guanacos were taken from Iriarte et al. (1991) and of rheas from Fjeldsa and Krabbe (1990). Average body mass of different passerine species was obtained from the literature (Fjeldsa and Krabbe, 1990).

Densities and body sizes of small mammals (<100g body mass) were obtained from an ongoing study of micro-habitat use by cricetine rodents (Corley et al., 1995; Novaro, 1991). These authors used mark-recapture techniques to evaluate densities of seven species of small rodents and one marsupial during June and July (late fall and early winter) of 1988 through 1992 on different habitats of La Rinconada, Catan Lil, Collun Co, and two other neighboring sheep ranches (Corley et al., 1995). No significant differences

in small-mammal densities were found among years in two steppe habitats sampled between 1989 and 1992, and between 1988 and 1990, respectively (Corley et al., 1995).

Minimum densities of the hairy armadillo, Chaetophractus villosus, the most abundant edentate in the study area, were estimated during the fall and winter of 1993 on one site in Collun Co and two sites in Cerro de los Pinos ranch. Armadillos were captured intensively during several weeks using 50 leg-hold traps baited with carrion (traps were set to capture culpeo foxes, Chapter 2), individually marked, and released, until no new captures were recorded. I estimated the size of the area of effect of the traps by adding a border strip of width equal to the diameter of the average home range (Wilson and Anderson, 1985; Seber, 1982) of the small hairy armadillo (C. vellerosus) around each capture area. The small hairy armadillo is the only similarly-sized edentate that occurs in similar habitats for which home-range size data are available (Gregeor, 1980; Redford and Eisenberg, 1992). I captured 11, 18, and 7 different hairy armadillos in 1.53, 0.87, and 0.61-km² areas, respectively. Average body mass of hairy armadillos was obtained from captured animals. No

data were available on the less abundant edentate, Zaedyus pichiy. Annual trends in edentate density were evaluated with track counts in 240 scent stations (Roughton and Sweeny, 1982) operated each winter between 1989 and 1994 in the six ranches (Chapter 2).

Carrion of medium- and large-bodied species. Density of carcasses of hare, sheep, cattle, red deer, and guanaco were obtained from a study conducted during the spring of 1995 and fall of 1996 (Aubone et al., 1996). These authors did carcass counts on 150 1-km-long line-transects (Marr et al., 1995) randomly located in Collun Co (cattle ranch), the section of La Rinconada where sheep are raised, and adjacent Collon Cura ranch, where guanaco are relatively abundant (Gader et al., 1987). Red deer occur on all three ranches. Spring and fall estimates were not significantly different so they were averaged. Average body mass of each species was used to calculate overall carrion biomass.

Relative biomass of prey. Fall-winter biomass of sheep, cattle, and hares on the different ranches were averaged for the entire study area, using weighted averages based on the relative size of each ranch. Biomasses of other prey were not available for every ranch, and they were

assumed to be similar among ranches due to the similarity of habitats. Carrion biomass was also not available for all ranches, but because total livestock biomass is similar among ranches, and livestock is the main component of carrion biomass (Aubone et al., 1996), I extrapolated the carrion biomass estimate to the entire study area. Finally, no data on yearly trends of carrion availability were obtained. However, reports from ranchers indicate that stocking rates and livestock mortality did not change significantly during the study period, so I assumed that carrion biomass remained constant between 1989 and 1994.

Expected proportions of prey used by carnivores were generated from the relative biomass of each prey. Availability of prey for each carnivore was estimated based on the assumed ability of each species to capture and kill prey. Juvenile and young sheep, hares, small mammals, hairy armadillos, passerine birds, and rheas were assumed to be available to culpeo foxes. Only hares, small mammals, hairy armadillos, and passerine birds were available to chillas and Geoffroy's cats. Young cattle and all previously enunciated prey were assumed to be available to pumas.

Data Analysis

Annual and seasonal trends in culpeo diet. Relative biomass of prey in stomach contents of culpeos during different years and seasons were compared using the von Mises test for continuous proportions (Stephens, 1982; Maehr and Brady, 1986). When significant differences were detected ($P < 0.05$), successive yearly or seasonal diets were compared using the Tukey's W -test with experimentwise and comparisonwise error rates $E = 0.05$ and $\alpha = 0.05/n$ (where n was the number of comparisons performed) respectively (Federer, 1955; Ott, 1988:446). Food habits of culpeos based on feces were compared among seasons with the log-likelihood ratio test for contingency tables (Sokal and Rohlf, 1995). Small sample sizes on food habits of other carnivores precluded statistical analyses among seasons and years.

Annual and seasonal trends in prey densities. Annual and seasonal trends in hare densities and annual trends in red deer and small mammal densities were analyzed using program CONTRAST (Hines and Sauer, 1989). Annual trends in densities of edentates were studied using the Fisher Randomization test (Roughton and Sweeny, 1982). No

statistical comparisons were performed among the annual densities of cattle, horses, and sheep, because the data were accurate counts provided by the ranchers.

Prey selection by predators. Selectivity of prey by culpeos and chillas was studied by comparing proportions of biomass of prey in stomachs to proportions of prey available using overall MANOVA procedures based on an F test. When differences were significant, I tested for selection or rejection of individual prey with individual MANOVA tests for each prey (PROC GLM, SAS Institute Inc., 1996). Expected proportions were the proportions of biomass of each prey available to each carnivore species. Selection of prey by pumas and Geoffroy's cats could not be tested because proportions of biomass in their diet were estimated mainly from fecal samples. Selection of prey by skunks was not tested because I lacked data on availability of invertebrates, a major component of their diet.

Results

Food Habits

The main prey of the culpeo between 1989 and 1994 was the European hare (mean percent-biomass in stomachs was 50.2% for all years combined), followed by sheep (21.0%),

and carrion (12.3%; Table 4-1). Fall-winter food habits of culpeos changed significantly among years ($Z = 30.01$; d.f.₁ = 42; d.f.₂ = 1548; $P < 0.001$, Table 4-1). Pairwise differences between 1989 and 1990, 1990 and 1991, and 1993 and 1994 contributed most to the overall differences. Primary differences were due to changes in consumption of hares.

Seasonal changes in culpeo diet during 1993 and 1994 were significant ($Z = 4.20$; d.f.₁ = 17; d.f.₂ = 823; $P < 0.001$, Table 4-2) according to data obtained from stomachs but were not significant according to data from feces ($G = 1.26$; d.f. = 10; $P = 0.35$; Table 4-3). Main seasonal differences were due to increased consumption of hares and a decline in consumption of cricetine rodents during the spring and summer (Table 4-2).

The primary food item of chillas was carrion (mean percent-biomass in stomachs was 61.1%), followed by hares (14.6%) and cricetines (11.4%; Table 4-4). Skunks also primarily consumed carrion (54.3% biomass in stomachs), but preyed significantly on invertebrates, mainly beetle larvae (29.4%; Table 4-4). Sample size for the Geoffroy's cat diet was small, so I combined data from stomachs and feces.

Table 4-1. Percent biomass of prey of the culpeo fox in southern Neuquén Province, Argentina, during the fall and winter seasons, 1989-1994.

Prey	1989*	1990*	1991*	1992	1993*	1994*
Introduced mammals:						
European hare	72.5	37.9	53.7	48.4	51.8	33.4
Sheep	11.7	32.1	13.7	21.1	18.1	23.1
Carrión**	9.5	20.4	22.3	6.2	6.2	16.2
European rabbit	1.7	0.0	0.0	0.0	0.0	2.3
Native mammals:						
Cricetines	1.1	4.5	1.5	10.8	14.8	19.1
<u>Ctenomys</u>	1.9	tr	5.3	10.6	5.5	0.5
<u>Microcavia</u>	tr	4.7	2.2	0.0	0.0	0.0
Edentates	1.2	tr	0.0	2.0	tr	2.0
Unidentified mammals	0.3	tr	0.0	0.8	0.2	0.4
Birds:						
<u>Pterocnemia</u>	0.0	0.4	0.0	0.0	0.0	0.0
Unidentified birds	tr	tr	1.3	0.1	3.3	2.9
Lizards:	0.0	tr	0.0	0.0	tr	0.1
Number of prey items	63	85	51	64	112	128
Number of stomachs	49	61	32	33	65	52
Percentage of stomachs with:						
beetles	0.0	2.0	0.0	0.0	0.0	0.0
seeds	0.0	0.0	0.0	0.0	0.0	0.0

Table 4-1--continued.

* Indicates significant differences with following winter ($W_{89-90} = 0.14$, $P < 0.01$; $W_{90-91} = 0.15$, $P < 0.01$; $W_{91-92} = 0.27$, $P < 0.01$; $W_{93-94} = 0.11$, $P < 0.01$). $W_{92-93} = 0.87$, $P > 0.05$.

** from introduced mammals (cattle, horse, sheep, and red deer) in all cases except 90 g from guanaco in one stomach in 1994.

tr = trace, $< 0.1\%$.

Table 4-2. Percent biomass of prey in culpeo fox stomachs in southern Neuquén Province, Argentina, during all seasons, 1993-1994.

Prey	winter*	spring	summer*	fall	total
Mammals:					
Hare	52.1	71.0	60.0	42.9	56.5
Sheep	23.0	20.2	23.8	13.4	20.1
Carrion	7.0	4.2	6.5	20.2	9.5
Cricetines	9.4	3.5	4.3	18.8	9.0
<u>Ctenomys</u>	8.0	0.0	0.0	0.0	2.0
Edentates	0.1	0.0	0.0	0.0	tr
Unidentified mammals	0.0	0.1	5.2	0.6	1.5
Birds:	0.1	1.1	0.0	4.0	1.3
Lizards:	0.0	0.0	0.2	0.2	0.1
Number of prey items	83	32	27	69	211
Number of stomachs	47	16	12	31	106
Percentage of stomachs with					
Beetles	0.0	0.0	0.0	0.0	0.0
Seeds	0.0	0.0	0.0	0.0	0.0
Mean mass of vertebrate prey (g)					457

* Indicates significant differences with following season: $W_{win.-spr.} = 0.29$, $P < 0.01$; $W_{sum.-fall} = 0.33$, $P < 0.01$. $W_{fall194-win.93} = 0.24$, $P < 0.05$. $W_{spr.sum.} = 0.94$, $P > 0.05$.

tr = trace, $< 0.1\%$.

Table 4-3. Percent occurrence of prey in culpeo fox feces in southern Neuquén Province, Argentina, during all seasons, 1993-1994.

Prey	winter	spring	summer	fall	total*
<hr/>					
Mammals:					
Hare	45.1	43.1	56.0	52.4	49.1
Sheep	3.7	1.7	0.0	3.5	2.2
Carrion	11.0	3.4	5.2	1.8	5.4
Cricetines	34.1	39.7	31.3	32.4	34.4
<i>Ctenomys</i>	1.2	6.0	1.5	3.5	3.1
Edentates	1.2	0.0	0.7	0.6	0.6
Unidentified mammals	0.0	3.4	0.0	1.8	1.3
Birds:	2.4	1.7	4.5	4.1	3.2
Lizards:	1.2	0.9	0.7	0.0	0.7
Number of vertebrate prey items	82	116	134	170	502
Number of feces	50	83	90	112	335
Percentage of feces with					
Beetles	2.0	3.6	14.4	1.8	5.7
Seeds	4.0	1.2	12.2	7.1	6.6

* No significant differences were found among seasons ($G = 6.9$; $P = 0.15$).

tr = trace, < 0.1%.

Table 4-4. Food habits of chillas, skunks, and Geoffroy's cats in southern Neuquén between 1989 and 1994. F = total frequency (in feces and stomachs), O = % occurrence (in feces and stomachs), M = % in mass (in stomachs).

Prey type	Chilla			Skunk			Geoffroy's		
	F	O	M	F	O	M	F	O	M**
Hare	9	14.5	14.6				3	13.6	
Carrión *	16	25.7	61.1	8	4.8	54.3	2	9.1	tr
Edentate	3	4.8	0.8						
Caviidae	2	3.2	6.5						
Ctenomyidae									
Cricetidae	14	22.6	11.4	1	0.6	0.1	14	63.6	97.0
Marsupials									
<i>Thylamys pusilla</i>	2	3.2	tr						
Unidentified mammals	5	8.1	0.5	1	0.6	tr			
Birds	1	1.6	2.5				3	13.6	3.0
Reptiles									
Lacertilia	3	4.8	0.5	3	1.8	4.4			
Colubridae									
Arthropods									
Coleoptera	6	9.7	1.3	7	4.2	1.0			
Coleoptera larvae				117	70.9	29.4			
Scorpions				7	4.2	7.1			
Aracnids				3	1.8	0.4			
Unidentified arthropods				5	3.0	1.0			
Earth worms				13	7.9	2.2			
Plant matter	1	1.6	tr						
Number of prey	62			165			13 (feces) 9 (stomachs)		
Number of stomachs	42			25			3		
Number of feces							7		
Mean mass of vertebrate prey (g)	147			12			56		

* Includes sheep, hare, red deer, cattle, and horse.

** Based on data from stomachs.

tr = trace, < 0.1%.

Table 4-5. Food habits of pumas in southern Neuquén during 1993 and 1994. F = total frequency (in feces), O = % occurrence (in feces), FS = frequency of occurrence (of identifiable prey found in feces), W = body mass (kg) of prey, CF = correction factor (Ackerman et al., 1984), RB = relative biomass consumed (%), RN = relative numbers consumed (%), M = % biomass (in stomachs).

Prey	F	O %	FS %	W** kg	CF kg/scat	RN %	RB %	M %
Introduced:								
Cattle or Horse	4	4.0	5.9	100.00	5.48	0.4	8.9	tr
Red deer	17	17.2	25.0	115.00	6.01	1.7	41.7	38.4
Sheep								
Wild boar	1	1.0	1.5	78.00	4.71	0.1	1.9	
Unidentif. ungulate	2	2.0						
Hare	54	54.5	79.4	3.44	2.10	62.4	46.3	61.6
Native:								
Hairy armadillo	1	1.0	1.5	2.99	2.08	1.3	0.9	
Caviidae								
Ctenomyidae	2	2.0	2.9	0.16	0.16	3.8	0.1	
Cricetidae	14	14.1	20.6	0.02	0.02	26.5	0.1	
Birds	1	1.0	1.5	0.06	0.06	1.9	tr	
Reptiles								
Colubridae	1	1.0	1.5	0.10	0.10	1.9	tr	
Plant matter	2	2.0						
Total	99	99.8	142.7			99.0	99.9	
Number of prey	97							5
Number of feces	70							
Number of stomachs	4							
Mean mass of vertebrate prey (kg)				3.16				

** References for body mass of prey were: juvenile cow or horse: C. Rambeaud, CEAN (local wildlife agency), pers. comm.; deer: C. Rambeaud, CEAN, pers. comm.;

Table 4-5--continued.

wild boar: L. Govetto, Argentine National Parks Service, pers. comm.; hare: Bonino & Bustos, 1994; hairy armadillo: this study; Ctenomyidae: Pearson & Christie, 1985; cricetidae: this study; birds: Fjeldsa and Krabbe, 1990; colubridae: M. Funes, CEAN, pers. comm.

tr = trace, < 0.1%.

Geoffroy's cats prey primarily on cricetines, and to a lesser extent on hares and birds (Table 4-4).

Primary food items of pumas were hares (mean percent-biomass was 46.3%, based on corrected proportions consumed) and red deer (41.7%; Table 4-5). Cricetines represented 26.5% of numbers of prey consumed by pumas, but only 0.1% of biomass consumed.

Prey Availability

Relative biomass of prey. Introduced (domestic and wild) species comprised 94% of the total biomass of herbivores and omnivores in the study area during the fall and winter seasons (Figure 4-1). Overall sheep density remained stable between 1989 and 1993, and declined 18% in 1994 when most sheep were removed from Cerro de los Pinos ranch (Table 4-6). Cattle density remained stable between 1989 and 1994 (Table 4-7). Hare densities changed significantly between 1989 and 1994 throughout the study area ($\chi^2 = 20.3$, $df=5$, $P=0.03$; Table 4-6), declining to ca. one third of their initial density.

Native species comprised the remaining 6% of the herbivore biomass in the study area (Figure 5-1 and Table 4-7). No significant changes in guanaco and lesser rhea

abundances were apparent from interviews with local people and counts on diurnal transects. Relative densities of edentates remained stable between 1989 and 1994 ($P > 0.42$, Table 4-6).

Biomass of introduced species and their carrion was 80, 78, 78, and 82% of the total biomass of prey available to culpeos, chilla foxes and Geoffroy's cats, and pumas, respectively during fall and winter (Table 4-8). Introduced wild species (hare and deer) comprised 11% of the total biomass of introduced species (Table 4-8).

Seasonal trends. Density and biomass of sheep increased during the spring, when lambs were born (Table 4-9). Hare densities did not change significantly among seasons during 1993 and 1994 ($\chi^2=0.9$, $df=3$, $P>0.05$; Table 4-9).

Selection of Prey

Overall selectivity. Culpeo and chilla food habits during fall and winter differed significantly from the biomass of available prey (Wilks' Lambda = 0.024 and 0.493, respectively, $P < 0.0001$). Culpeos consumed hares more than expected according to their availability, and carrion, edentates, and birds less than expected (Tables 4-1 and

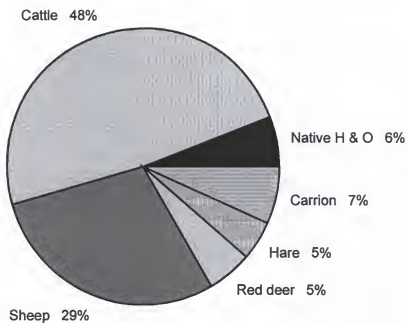


Figure 4-1. Relative biomass of introduced species (domestic and wild) and native herbivores and omnivores (Native H & O) on a 1,420-km² area in southern Neuquen. Carrion includes primarily introduced species.

Table 4-6. Fall-winter absolute densities (ind/km²) of European hares and sheep and relative densities (percent of scent stations visited) of edentates in steppe habitat of southern Neuquén between 1989 and 1994. Means followed by the same letter are significantly different ($P < 0.05$). No statistical test was performed on the sheep data.

Year	1989	1990	1991	1992	1993	1994	Overall
Hare density	76.11 ^a	56.81 ^a	47.04	34.39	35.83	25.78 ^a	46.00
SD	31.86	29.07	11.05	10.28	18.54	15.45	25.85
Sheep** density	26.29	25.16	25.66	25.57	24.67	20.16	24.59
SD	16.92	13.79	14.90	13.23	13.30	14.61	2.23
Edentate density	3.1	0.9	3.4	2.3	1.3	2.0	2.1

* Hare density estimates were available only for La Rinconada, Catan Lil, Los Remolinos, and La Papay ranches in 1990. To estimate the overall hare density in 1990 I assigned to Collun Co and Cerro de los Pinos the mean hare densities in those ranches between 1989 and 1991.

** Overall density for the entire study area, including area of intermixed cattle ranches.

Table 4-7. Density (ind/km²) and body mass (kg) of introduced and native herbivores and omnivores and of carrion of dominant species in steppe habitat of southern Neuquén.

Prey	Density	Body mass ^a	Source
<u>Introduced domestic:</u>			
Cattle and horses	4.87± 4.16	475-190-80	Ranchers
Sheep	24.59± 2.23	47-25-3	Ranchers
<u>Introduced wild:</u>			
European hare	46.00±25.85	3.4-1.2	This study, Amaya (1984), and Bonino & Bustos (1994)
Red deer	1.58±0.30	115-75-30	This study and wildlife agency
<u>Native:</u>			
Guanaco	0.67±0.13	120-80-30	Wildlife agency and Iriarte et al. (1991)
Small mammals ^(b)	2422.91±1597	0.023	Corley et al. (1995)
Hairy armadillo	13.11±6.88	2.99	This study
Lesser rhea	0.62±0.28	15-6-1	Wildlife agency
Passerine birds	264.08±112	0.06	Travaini et al. (1989)
<u>Carrion:</u>			
Large ungulates ^(c)	9.73±2.36		Aubone et al. (1996)
Sheep	2.30±0.54		Aubone et al. (1996)
Hare	0.55±0.21		Aubone et al. (1996)

Table 4-7--continued.

^a Masses were obtained for adult, yearling, and juvenile large-ungulates and rheas, adult and young hares. One average estimate was used for other species.

^b Includes seven species of cricetine rodents (Abrothrix longipilis, A. olivaceus, A. xanthorhinus, Akodon iniscatus, Eligmodontia morgani, Oligoryzomys longicaudatus, and Phyllotis xanthopygus) and the small marsupial Thylamys pusilla. Body mass was obtained as the average from all individuals captured.

^c Includes cattle, horses, and red deer.

Table 4-8. Overall biomass of introduced and native herbivores and omnivores and relative biomass available to culpeos, chillas, Geoffroy's cats, and pumas during fall and winter seasons in steppe habitat of southern Neuquén.

	Overall	Culpeo	Chilla & Geoffroy's	Puma
Introduced:				
Cattle & horse	48.5			13.1
Sheep	28.9	20.8		23.3
Red deer	5.3			24.5
Hare	4.6	24.4	31.5	21.3
Native:				
Guanaco	2.3			1.3
Small mammals	1.6	8.6	11.1	7.5
Hairy armadillo	1.1	6.0	7.8	5.3
Passerine birds	0.5	2.4	3.2	2.1
Lesser rhea	0.4	1.9		1.7
Carrion	6.7	35.8	46.4	--*
Total kg/km ²	3442	649	502	744

* I assumed pumas do not consume carrion.

Table 4-9. Seasonal densities (ind/km²) of European hares and sheep in steppe habitat of southern Neuquén during 1993 and 1994. Mean hare densities were not significantly different among seasons ($P > 0.05$). No statistical test was performed on the sheep data.

Season	winter	spring	summer	fall	annual
Hare density*	51.21	46.82	45.10	46.80	47.48
SE	2.53	3.92	14.56	18.07	5.00
Sheep** density	24.67	32.44	27.98	20.16	26.31
SE	13.30	14.01	13.60	14.61	13.88

* seasonal densities based on transect counts only at C. de los Pinos and Collun Co ranches.

** Overall density for the entire study area, including area of intermixed cattle ranches.

Table 4-10. Prey selection by culpeos in southern Neuquén, Argentina, during fall and winter, 1989-1994, and during spring and summer, 1993-1994. Percentages of biomass available and in the diet are only for prey for which availability data were obtained. Percentages of prey in the diet were compared to percentages expected according to availability using a Manova test (SAS Institute, Inc., 1996). T: annual overall, H: hare, L: young sheep, C: carrion, R: cricetines, E: edentates, B: passerine birds and lesser rhea. Percent biomass of diet considered out of overall diet is indicated between parentheses.

	Prey	Available	Diet	Wilks' Lambda	d.f.1	d.f.2	P level
Fall-winter							
1989	T			0.343	5	32	0.0001
(98)	H	35.7	76.0	0.632	1	36	0.0001
	L	17.7	12.0	0.972	1	36	0.3177
	C	30.4	9.7	0.362	1	36	0.0001
	R	7.3	1.1	0.999	1	36	0.9759
	E	5.1	1.2	0.990	1	36	0.5486
1990	T			0.024	5	38	0.0001
(95)	H	29.4	39.8	0.957	1	42	0.1759
	L	20.1	33.7	0.905	1	42	0.0420
	C	33.0	21.4	0.832	1	42	0.0057
	R	7.9	4.7	0.995	1	42	0.6590
	E	5.6	tr	0.029	1	42	0.0001
1991	T			0.000	5	22	0.0001
(92)	H	24.3	58.1	0.816	1	26	0.0229
	L	20.9	14.8	0.999	1	26	0.8760
	C	35.8	24.2	0.807	1	26	0.0192
	R	8.6	1.6	0.989	1	26	0.5960
	E	6.0	0.0	0.000	1	26	0.0001
1992	T			0.246	5	22	0.0001
(89)	H	19.0	54.6	0.821	1	26	0.0246
	L	23.1	23.8	0.998	1	26	0.8472
	C	37.9	7.0	0.258	1	26	0.0001
	R	9.1	12.2	0.886	1	26	0.0786
	E	6.4	2.2	0.998	1	26	0.8159

Table 4-10--continued.

	Prey	Available	Diet	Wilks' Lambda	d.f.1	d.f.2	P level
1993	T			0.294	5	48	0.0001
(90)	H	19.7	55.0	0.799	1	52	0.0007
	L	21.5	19.2	0.999	1	52	0.8760
	C	38.5	6.6	0.758	1	52	0.0002
	R	9.2	15.7	0.873	1	52	0.0082
	E	6.5	0.1	0.374	1	52	0.0001
1994	T			0.493	5	44	0.0001
(96)	H	16.5	36.0	0.880	1	48	0.0138
	L	18.6	23.3	0.984	1	48	0.3826
	C	42.5	16.4	0.526	1	48	0.0001
	R	10.2	19.3	0.881	1	48	0.0142
	E	7.2	2.0	0.912	1	48	0.0368
Spring-summer							
1993-1994							
(93)	T			0.000	5	22	0.0001
	H	18.2	68.0	0.570	1	26	0.0017
	L	27.3	22.2	0.993	1	26	0.7205
	C	35.6	5.3	0.563	1	26	0.0015

tr = trace, < 0.1%.

4-8). Chillas consumed carrion more than expected and hares and edentates less than expected (Tables 4-4 and 4-8).

Pumas seem to consume red deer and hares more than expected according to their availability and sheep, guanaco, and small prey less than expected (Tables 4-5 and 4-8).

Annual selectivity: I conducted an evaluation of annual selectivity of prey by culpeos because their diet was shown to differ significantly among years (Table 4-1). Passerine birds were excluded from this analysis because no data were available to determine annual trends in their densities. Culpeo diets differed significantly from the availability of prey biomass during all years ($P < 0.0001$; Table 4-10). In spite of the decline in hare density between 1989 and 1994, culpeos consumed hares more than expected during all years ($P < 0.025$) except for 1990, the first year of the hare decline ($P = 0.176$). Young sheep were consumed more than expected only during 1990 ($P = 0.042$). Carrion was consumed less than expected during all years ($P < 0.019$). Cricetines were consumed according to their availability between 1989 and 1992 ($P > 0.079$), and more than expected in 1993 and 1994 ($P < 0.014$). Edentates

were consumed less than expected during four of the six years ($P < 0.037$; Table 4-10).

Seasonal selectivity: I conducted an evaluation of seasonal selectivity of prey by culpeos because their diet was shown to differ significantly among seasons (Table 4-2). Cricetines, edentates, and passerine birds were excluded from the analysis because no data were available to determine seasonal trends in their densities. During the spring and summer of 1993-1994 culpeos preyed on hares more than expected ($P = 0.0017$) and consumed carrion less than expected ($P < 0.0015$) according to their availability. Culpeos did not prey more on sheep in spring and summer, in spite of their increased availability due to the birth of lambs during the spring (Tables 4-9 and 4-10).

Discussion

Carnivore Food Habits

Introduced prey and their carcasses dominated the diet of the carnivores studied in northwestern Patagonia. These carnivores appeared to consume their prey opportunistically, because the proportions of each prey in their diets were similar to the relative biomass of prey available. Carrion from domestic ungulates and hares was the main component in

the diet of chillas and skunks. Introduced prey represented 71.2 and 98.9% of the biomass in the diet of culpeos and pumas, respectively, and carrion was also significant in the diet of culpeos. Among introduced prey, predation on wild species (hare and deer) dominated over domestics, although the wild species represented only a small fraction (11%) of the total biomass of introduced species available. The small contribution of native prey was related to their small representation in the overall herbivore biomass.

Overall, introduced prey were more important in the carnivore diets in this study than in any other study previously conducted in South America. Primary prey items of culpeos and chillas in Chile were small mammals and introduced lagomorphs (Johnson and Franklin, 1994a; earlier data reviewed in Redford and Eisenberg, 1992). Pumas preyed heavily on plains vizcachas (Lagostomus maximus) and wild boars in Lihue Calel National Park (Branch et al., 1996), on guanacos and European hares in Torres del Paine National Park (Iriarte et al., 1991), and on sheep and hares in a ranch adjacent to the latter park (Yanez et al., 1986). The food habits of the common hog-nosed skunk were only known

from anecdotal information, and they included arthropods and frogs (Barlow, 1965; cited in Redford and Eisenberg, 1992).

Prey Availability

The native mammals and birds studied represented only 5.0 and 0.9%, respectively, of the total herbivore biomass at this site in northwestern Patagonia. Most of the biomass of native animals corresponds to species of small body sizes. Small rodents and marsupials and medium-sized hairy armadillos combined represented ca. 54% of the native-mammal biomass in Patagonia. Densities of medium-sized hystricognath rodents (Ctenomys sp., Myocastor coypus, Microcavia australis, and Lagidium viscacia), were not estimated, but all of these species have highly patchy distributions (Pearson, 1995; Walker et al., 1995) and their overall contribution to the mammal biomass is probably small, as inferred from their small representation in the carnivores' diets in this study.

The major significance of species of small body sizes to the biomass of the native fauna in this area of Patagonia was due to low densities of guanacos and lesser rheas, the only native large animals in the Patagonian steppe. Guanacos and rheas probably were the dominant herbivores

before the introduction of livestock and exotic lagomorphs and deer (Crespo, 1975; Johnson et al., 1990). Overall current densities of guanacos and rheas throughout most of the 450,000 km² of Argentinean Patagonia probably are similar to those reported in this study (Garrido, 1984). Low guanaco and rhea densities and high hare density may explain the small mean mass of vertebrate prey consumed by pumas in this study, the lowest reported for the species (Iriarte et al., 1990; Oliveira, 1994) with the exception of pumas in the Paraguayan Chaco (Taber et al., 1997).

Thus the native large-bodied species appear to be ecologically extinct (Estes et al., 1989) in this area of Patagonia with respect to their role as prey and source of carrion for native carnivores. Only some small- and medium-sized mammals (cricetine rodents and edentates) still play a significant role in predator-prey interactions with small- and medium-sized carnivores (foxes, small cats, and skunks) in this region, as they do in protected areas in Chile.

The role of guanacos and rheas in these interactions has been replaced by red deer and European hares. The biomass of deer and hares combined was 68% larger than that of all native species studied in northwestern Patagonia

(Table 4-8). These exotics dominated the diet of the larger-sized pumas and culpeos, and they or their carcasses represented an important proportion of the diet of the small chilla foxes and skunks.

This shift is similar to the changes observed in semi-arid regions of Australia, where exotic herbivores and omnivores have reached high densities and biomasses (Corbett, 1995; Ridpath, 1991). The main difference between predator-prey interactions in semi-arid Australia and Patagonia is that in Australia the dominant predators are also exotic (dingoes and red foxes), whereas in Patagonia they are all native. However, as in Australia (Newsome, 1990; Pech et al., 1992), predators in Patagonia may play an important role in regulating mammalian prey populations (including exotics), at least during periods when prey densities are low (Walker and Noy-Meir, 1982; Holling, 1988).

Understanding these predator-prey interactions in Patagonia could have important management and conservation implications. Introduced wild and feral mammals increase herbivore-grazing pressure and may contribute to widespread habitat degradation by livestock in Patagonia. European

rabbits are common along river valleys in northwestern Patagonia, rabbits and red deer are still expanding their ranges (Funes, 1996), and wild boars are locally abundant in the more humid and productive mallines. Furthermore, six other species of ungulates have been introduced into Neuquén Province in recent years (Funes, 1996) and poor regulation makes future introductions likely.

Culpeo Interaction with European Hares and Possible Ecosystem Impact

The role of predators as regulators of prey populations depends on their functional and numerical responses to the prey (Holling, 1959). Functional and numerical responses of culpeo foxes to changes in prey availability vary among sites and type of prey (reviewed by Novaro, 1997). A functional response of prey switching (Jaksic and Simonetti, 1987) was recorded in central and southern Chile and Argentina. During seasons when availability of small mammals or hares declined, culpeos consumed increasing numbers of arthropods and fruit (Castro et al., 1994; Ebensperger et al., 1991; Jaksic et al., 1980; Johnson and Franklin, 1994a) or sheep (Crespo and De Carlo, 1963). Culpeos did not display a functional response in their diet

to marked changes in Octodon degus abundance, maintaining a strong preference for this species. However, culpeos displayed a significant numerical response following fluctuations in abundance of O. degus at Fray Jorge National Park in north-central Chile (Jaksic et al., 1993). Finally, culpeos did not show a functional or a numerical response during a decline of their rodent prey (mainly O. degus and Abrocoma bennetti) at Aucó in north-central Chile (Jaksic et al., 1992, 1996; Martínez et al., 1993).

In this study, culpeos did not display a numerical response during the hare decline (Chapter 2). However, culpeos increased the consumption of alternative prey, namely sheep and carrion in 1990 and 1991, cricetine rodents in 1992-1994, Microcavia in 1990, Ctenomys sp in 1991-1993, and birds in 1993-1994.

The increased consumption of alternative prey could be due to changes in the availability of these prey and not to a decline of the main prey. However, sheep and carrion availability remained stable throughout the study, so increased consumption of these food items was probably a direct consequence of the hare decline. Higher culpeo consumption of cricetines during 1990, 1992, and 1993 also

occurred likely as a consequence of the hare decline. Cricetine availability probably remained stable between 1989 and 1993, but their density may have increased significantly in 1994. Fall and winter track counts of cricetines on scent-stations remained stable between 1989 and 1993 at an average of 3.3% of stations visited, but increased to 10.2% in 1994. Cricetines were also most common in the culpeo diet during this year. However, culpeos continued to prey selectively on hares in spite of a significant reduction in hare density.

Thus, culpeo predation may have a significant effect on the regulation of hare numbers when this prey is at low densities. Culpeos are the most abundant terrestrial predators in this region (Novaro and Funes, unpubl. data), but other predators also consume large numbers of hares. These include pumas, chilla foxes, and >10 species of avian predators (Travaini et al., unpubl. data), some of which prey primarily on hares.

These findings also have implications for the status of small and medium-sized vertebrates in the region. First, culpeos, and perhaps other terrestrial and avian predators (A. del Valle, pers. comm.), have increased their densities

in the region in recent decades (Crespo and de Carlo, 1963), probably as a result of the high stocking rates of introduced herbivores, which are well over the carrying capacity of this semi-arid ecosystem. An increasing trend in culpeo density is apparent in recent years, but in this case probably due to the reduction in hunting pressure from humans (Chapter 2).

The native herbivore assemblage already experiences a significant reduction in their access to plant resources due to high overlap in their diets with introduced species (Brandani et al., 1982; Bonino et al., 1986). Furthermore, some of the native species (primarily guanacos, rheas, armadillos, and mountain vizcachas) are intensively hunted for food by local people (Novaro and Funes, unpubl. data). During years of low density of hares, the impact of carnivore predation could add a significant source of mortality to the populations of native herbivores and omnivores.

Secondly, selective consumption by culpeos and other predators can have significant effects on populations of small rodents (Meserve et al., 1996). Competition among small-mammal species can be influenced by the impact of

predation (Meserve et al., 1996). Both culpeos (reviewed in Novaro, 1997) and chillas (Martinez et al., 1993) selectively prey on certain rodent species. In the study area the most common cricetine (Eligmodontia morgani) is rarely taken, and the species of the genus Abrothrix are overrepresented in the culpeo diet (Novaro, 1991; Corley et al., 1995).

Therefore both the total and relative abundances of native herbivores and omnivores could be affected directly by competition with introduced species and by increased predation during declines of exotic species. This is a similar interaction to that described by Bergerud (1983) in Newfoundland, where abundance of arctic hare declined after the introduction of the snowshoe hare. The role of predators in this case could be similar to that of a "predator release" scenario (Ball et al., 1995; Soule et al., 1988), with perhaps devastating effects of further reduction and local extinction of some native prey.

Overall Conclusions

In summary, the following conclusions were obtained from this study:

1. The diets of medium and large-bodied carnivores (culpeo foxes and pumas) comprised almost exclusively introduced species, whereas the diets of small carnivores (chilla foxes and skunks) were mainly carrion from introduced species in this area of the northwestern Patagonian steppe.

2. The native large-bodied species (guanacos and rheas) are ecologically extinct with respect to predator-prey interactions in the area, and perhaps in most of Argentinean Patagonia. Cricetine rodents and edentates are the only native prey that play a significant role in the diets of small and medium-sized carnivores.

3. Predation by culpeos and other carnivores may regulate populations of introduced hares, thus reducing competition between hares and native herbivores, but increased predation on native prey during periods of low hare abundance may result in significant periodic reductions of the abundance of native herbivores and omnivores.

CHAPTER 5 CONCLUSIONS

Culpeo Harvest and Population Dynamics

During my study I concluded that the structure of the landscape and the ability of culpeo foxes (Pseudalopex culpaeus) to disperse between unhunted and hunted areas are essential for their long term persistence in northwestern Patagonia (Chapter 2). This type of population process closely resembles a source-sink system induced by habitat heterogeneity (Lidicker, 1975; Pulliam, 1988). My findings on culpeos indicate that source-sink dynamics can be the result of direct human disturbance and not only a consequence of heterogeneous habitat quality in the landscape (Hanski and Simberloff, 1996). Source-sink dynamics may be common in other landscapes where hunting is intense and spatially heterogeneous. In the case of culpeo populations, my findings also suggest that conservation measures should be taken at the landscape level and not by attempting to affect demographic rates alone, as is done traditionally in wildlife management.

Based on the limitations of wildlife management in Patagonia and my findings about culpeo population dynamics, I concluded that a harvest system regulated by spatial controls (McCullough, 1996; Joshi and Gadgil, 1991) is more likely to prevent overharvest than one that attempts to regulate the size of the harvest. An approach to sustainable harvest by spatial control requires that a certain proportion and size of areas be kept as refugia in a mosaic of hunted and unhunted areas. Without spatial controls, the proportion of unhunted patches in this mosaic could decline to a level that would make regional populations of culpeos collapse (Chapter 3). Most of Patagonia has similar land-use practices to the ones in my study area, with the size of ranches varying according to primary productivity and land tenure. Harvest refugia could be designated on cattle ranches and on more inaccessible areas near sheep ranches. This would allow high connectivity between hunted and unhunted areas. Limited enforcement resources could be concentrated on enhancing culpeo productivity in source areas, by controlling poaching and reducing populations of feral dogs.

However, when implementing a spatial control strategy, the quality of habitat on sheep ranches and the proportion of land on sheep and cattle ranches should be monitored closely. Sink populations that occupy a large proportion of the habitat available in a source-sink system may contribute significantly to the regional population size and stability (Howe et al., 1991). Therefore, management for sustainable use of culpeos should include protecting habitat quality on hunted areas, particularly considering that these are usually sheep ranches where overgrazing and habitat degradation are more prevalent. Because of the two problems described (habitat degradation and changes in the proportion of unhunted area), I believe that sustainable use of culpeos may be achieved only if habitat deterioration on sheep ranches is reduced simultaneously with the implementation of a spatial control strategy.

Culpeo Management through Spatial Control:

A Dynamic Mosaic

The mosaic of sheep and cattle ranches in northwestern Patagonia is dynamic, with landowners periodically changing land-use practices in response to changes in wool and meat prices. I used a population simulation model to predict the

threshold level in the ratio of land on hunted to unhunted ranches where a collapse would occur if cattle ranches were switched to hunted sheep ranches (Chapter 3). My findings indicate that this threshold level is relatively close to the current ratio in southern Neuquen Province, suggesting that changes from cattle to sheep raising on a small number of ranches would be sufficient to make the current harvest pressure on culpeos unsustainable.

For management purposes, the primary variable to monitor in this system is the proportion of area on cattle and sheep ranches. During the field study two ranches switched from sheep to cattle raising due to plummeting wool prices in the early 1990s. So the recent changes in the area were in the direction of a more sustainable harvest of culpeo populations. If wool prices increase or if beef prices decline, this trend could reverse quickly.

During the field study of culpeo demography (Chapter 2), fecundity, survival, and migration rates were estimated using small sample sizes, so biases of their means and standard deviations were likely. According to the results of the sensitivity analysis done using the culpeo simulation model, research efforts should concentrate on estimating

survival rates of adult culpeos accurately. Biases on fecundity, juvenile survival, and migration rate estimates would have a smaller influence on the predictions of culpeo population trends.

Density-dependent effects on vital rates also need further investigation. A better understanding of density dependent mechanisms in culpeo populations would allow researchers and managers to conduct longer-term simulations and predict the consequences of potential increases in reproduction as a result of reduced population density. If further studies of culpeo reproduction (with larger sample sizes and replicated landscape patches) confirm the pattern observed here (of similar reproductive rates on hunted and unhunted ranches), potential mechanisms responsible for this pattern should be investigated. Because of high connectivity among hunted and unhunted ranches, hunting may lower population densities on hunted as well as unhunted ranches. The effect of this reduced population density on reproductive rates could be similar on hunted and unhunted areas.

Finally, another aspect that should be studied further using simulation tools and knowledge of density dependent

mechanisms is the demographic significance of populations on hunted sheep ranches (Howe et al., 1991; Pulliam, 1988). The culpeo model developed in this study could be used to evaluate the effect of reduced carrying capacity in hunted areas on regional population stability.

Ecological Extinction of Native Herbivores and Omnivores in Patagonia

My study documents the first case of a native carnivore assemblage in which most carnivores rely primarily on introduced prey (Chapter 4). The replacement of native prey by introduced prey in Argentinean Patagonia is likely a consequence of the introduction of livestock and of wild lagomorphs and red deer (Cervus elaphus), the deterioration of pastures due to overgrazing by these exotic herbivores, and subsistence hunting of native species by rural people.

The native mammals and birds studied represented only ca. 6% of the total herbivore and omnivore biomass in the study area in northwestern Patagonia. Most of the biomass of native animals corresponded to species of small body sizes. Small rodents and marsupials and medium-sized edentates combined represented ca. 54% of the native-mammal biomass. Densities of other herbivores, such as medium-

sized hystricognath rodents, were not estimated but their overall contribution to the mammal biomass is probably not large, as inferred from their small representation in the carnivores' diets in this study.

The major contribution of species of small body sizes to the biomass of the native component of the fauna of this Patagonian site was due to low densities of guanacos (Lama guanicoe) and lesser rheas (Pterocnemia pennata), the only native large animals in the Patagonian steppe. Guanacos and rheas were probably the dominant herbivores before the introduction of livestock and exotic lagomorphs and deer (Crespo and de Carlo, 1963; Darwin, 1962). Overall current densities of guanacos and rheas throughout most of the 450,000 km² of Argentinean Patagonia are probably similar to those reported in this study (Garrido, 1984).

The native large-bodied species appear to be ecologically extinct (Estes et al., 1989) in this area of Patagonia with respect to their role as prey and source of carrion for native carnivores. Only some small- and medium-sized mammals (cricetine rodents and edentates) still play a significant role in predator-prey interactions with small- and medium-sized carnivores (foxes, small cats, and skunks,

Conepatus chinga) in this region, as they do in protected areas in Chile.

The role of guanacos and rheas in these interactions has been replaced by red deer and European hares. The biomass of deer and hares combined was 68% larger than that of all native species studied in northwestern Patagonia. These exotics dominated the diet of the pumas (Puma concolor) and culpeo foxes, and these species (live or carcasses) represented an important proportion of the diet of the small chilla foxes (P. griseus) and skunks.

This shift is similar to the changes observed in semi-arid regions of Australia, where exotic herbivores and omnivores have reached high densities and biomasses (Corbett, 1995; Ridpath, 1991). The main difference between predator-prey interactions in semi-arid Australia and the Patagonian steppe is that in Australia the dominant predators are also exotic (dingoes and red foxes), whereas in Patagonia they are all native. However, as in Australia (Newsome, 1990; Pech et al., 1992), predators in Patagonia may play an important role in regulating mammalian prey populations (including exotics), at least during periods

when prey densities are low (Walker and Noy-Meir, 1982; Holling, 1988).

Understanding these predator-prey interactions in Patagonia could have important management and conservation implications. Introduced wild and feral mammals increase herbivore-grazing pressure and may contribute to widespread habitat degradation in Patagonia. European rabbits are common along river valleys in northwestern Patagonia, rabbits and red deer are still expanding their ranges (Funes, 1996), and wild boars are locally abundant in the more humid and productive habitats. Furthermore, six other species of ungulates were introduced into Neuquen Province in recent years (Funes, 1996) and poor regulation makes future introductions likely.

Unfortunately there are no areas in the Patagonian steppe of Argentina today that are free of the effect of grazing by introduced domestic and wild species. Even most protected areas currently are subject to at least periodic grazing by livestock, and few sustain significant numbers of guanacos and rheas. In fact the largest populations of these native species occur inside private ranches, where they coexist with livestock. An important conservation

measure would be to re-create ecosystems in Argentinean Patagonia where native predators and native prey are the dominant components of the local fauna. This would allow the study of ecological processes that have been severely altered or suppressed (like the interaction between native predators and their prey, and between plants and native herbivores) and preserve examples of this unique and degraded ecosystem.

APPENDIX I
CAPTURE DATA AND FATE OF CULPEOS RADIO-TRACKED IN HUNTED
AND UNHUNTED RANCHES IN NEUQUEN BETWEEN JANUARY 23,
1993, AND MARCH 14, 1994.

Ranch	No fox	Sex	Age*	Capture or arrival date	Fate (until 3/14/94)	Death or censor date	Cause of death **	Dispersed to other / within ranch (hunted: H, or unhandled: UH)	Dispersal distance (km)	Reproduced (of females that lived through the rep. season) (litter size, u: unknown)
HUNTED										
C. Pinos	3	F	J	4-Feb-93	Died	5-Jul-93	H			-
C. Pinos	26	F	J	23-Apr-93	Died	2-Sep-93	H			-
C. Pinos	29	F	J	21-May-93	Died	9-Oct-93	H			yes (3)
C. Pinos	30a	F	J	22-May-93	Censored (d)	14-Jul-93		UH-Quemquemtreu	25	-
C. Pinos	4	M	J	6-Feb-93	Died	30-Mar-93	H			
C. Pinos	6	M	J	21-Feb-93	Died	27-May-93	H			
C. Pinos	8	M	J	1-Mar-93	Died	30-Mar-93	RK			
C. Pinos	25	M	J	22-Apr-93	Died	5-Jun-93	H			
C. Pinos	27	M	J	24-Apr-93	Died	17-Jun-93	H			
C. Pinos	28b	M	J	7-May-93	Censored (d)	5-Sep-93		H-Cantera	90	
C. Pinos	2	F	A	23-Jan-93	Lived	-				yes (3)
C. Pinos	7	F	A	1-Mar-93	Lived	-				no
C. Pinos	9c	F	A	18-Feb-94	Lived	-				-
C. Pinos	22	F	A	28-Feb-93	Lived	-				yes (3)
C. Pinos	5	M	A	8-Feb-93	Censored (la)	28-Mar-93				
C. Pinos	23	M	A	15-Mar-93	Died	13-Oct-93	H	within-C. Pinos	10	
C. Pinos	24	M	A	18-Mar-93	Lived	-				
Cantera	28b	M	J	25-Sep-93	Lived	-				
Corfone	15d	M	A	8-May-93	Died	10-Jul-93	H			

* J: juvenile; A: adult

** H: hunting; RK: vehicle collision; FD: feral dogs

a, b, c: indicates it is the same culpeo, before or after dispersal

la: loss of radio signal probably due to transmitter failure; d: dispersed; censored: left population

Ranch	No	Sex	Age*	Capture or arrival date	Fate (until 3/14/94)	Death or censor date	Cause of death **	Dispersed to other / within ranch (hunted: H, or unhunted: UH)	Dispersal distance (km)	Reproduced (of females that lived through the rep. season)
										(litter size, u:unknown)
UNHUNTED										
Collun Co	9c	F	J	15-Mar-93	Censored (d)	28-Jan-94		H-C. Pinos	15	no
Collun Co	13	M	J	18-Mar-93	Lived	-		UH-Collun Co	10	
Collun Co	14	M	J	18-Mar-93	Lived	-		UH-Collun Co	10	
Collun Co	18	M	J	2-Apr-93	Died	22-Nov-93	FD			
Collun Co	10	F	A	15-Mar-93	Died	15-Dec-93	FD			yes (u)
Collun Co	11	F	A	16-Mar-93	Lived	-				yes (5)
Collun Co	19	F	A	3-Apr-93	Lived	-				yes (3)
Collun Co	12	M	A	17-Mar-93	Lived	-				
Collun Co	15d	M	A	18-Mar-93	Censored (d)	17-Apr-93		H-Corfone	25	
Collun Co	16	M	A	26-Mar-93	Censored (1s)	13-May-93				
Collun Co	17	M	A	2-Apr-93	Lived	-				
Quemquemtreu	30a	F	J	14-Aug-93	Lived	-				no

* J: juvenile; A: adult

** H: hunting; RK: vehicle collision; FD: feral dogs

a, b, c: indicates it is the same culpeo, before or after dispersal

1s: loss of radio signal probably due to transmitter failure; d: dispersed; censored; left population

APPENDIX II
CAPTURE DATA AND FATE OF CULPEOS RADIO-TRACKED IN
FORMERLY HUNTED, HUNTED, AND UNHUNTED RANCHES IN
NEUQUEN BETWEEN MARCH 15, 1994, AND MARCH 14, 1995.

Ranch	No fox	Sex	Age *	Capture or arrival date **	Fate (until 3/14/95)	Death or censor date	Cause of death ***	Dispersed to other / within ranch (hunted: H, or unhunted: UH)	Dispersal distance (km)	Reproduced (of females that lived through the rep. season) (litter size, u: unknown)
FORMERLY HUNTED										
C. Pinos	39a	F	J	22-Jun-94	Lived	-	-			no
C. Pinos	44	F	J	10-May-94	Lived	-	-			no
C. Pinos	65	F	J	24-Apr-94	Censored (d)	9-Oct-94	-	Died during disp.		-
C. Pinos	45b	M	J	18-May-94	Censored (d)	5-Oct-94	-	H-Aquino	20	
C. Pinos	47	M	J	2-Jun-94	Lived	-	-			
C. Pinos	66	M	J	20-May-94	Died	1-Oct-94	PO			
C. Pinos	2	F	A	15-Mar-94	Lived	-	-			yes (u)
C. Pinos	7	F	A	15-Mar-94	Lived	-	-			yes (u)
C. Pinos	9	F	A	15-Mar-94	Lived	-	-			yes (u)
C. Pinos	22	F	A	15-Mar-94	Lived	-	-			yes (u)
C. Pinos	38	F	A	22-Apr-94	Lived	-	-			no
C. Pinos	24	M	A	15-Mar-94	Died	5-Oct-94	U			
C. Pinos	46	M	A	1-Jun-94	Lived	-	-			
HUNTED										
Aquino	45b	M	J	9-Nov-94	Died	1-Mar-95	H			
Cantera	28	M	A	15-Mar-94	Lived	-	-			

* J: juvenile; A: adult

** or beginning of study period

*** PO: poison; H: hunting; FD: feral dogs; HF: poacher; DD: domestic dogs; PU: puma; U: unknown

a, b, c: indicates it is the same culpeo, before or after dispersal

d: dispersed; lc: loss of collar; t: transient; censored; left population

Ranch	No	Sex	Age *	Capture or arrival date **	Fate (until 3/14/95)	Death or censor date	Cause of death ***	Dispersed to other / within ranch (hunted: H, or unhunted: UH)	Dispersal distance (km)	Reproduced (of females that lived through the rep. season) (litter size, u: unknown)
UNHUNTED										
Collun Co	39a	F	J	22-Apr-94	Censored (d)	16-Jun-94				
Collun Co	40	F	J	6-May-94	Censored (lc)	19-Aug-94		H-C. Pinos	25	-
Collun Co	41c	F	J	1-May-94	Censored (d)	23-Dec-94		UH-EI Porvenir	10	-
Collun Co	43	F	J	2-May-94	Died	15-Oct-94	FD			-
Collun Co	50	F	J	5-May-94	Lived	-				no
Collun Co	49	M	J	1-Jun-94	Censored (lc)	2-Nov-94				
Collun Co	11	F	A	15-Mar-94	Lived	-				yes (4)
Collun Co	19	F	A	15-Mar-94	Censored (lc)	15-Apr-94				-
Collun Co	35	F	A	27-Mar-94	Died	14-Aug-94	HP			-
Collun Co	36	F	A	5-Apr-94	Lived	-				yes (u)
Collun Co	42d	F	A	2-May-94	Censored (t)	23-Feb-95		UH-EI Porvenir	-	no
Collun Co	12	M	A	15-Mar-94	Died	28-May-94	DD			
Collun Co	13	M	A	15-Mar-94	Died	24-Mar-94	PU			
Collun Co	14	M	A	15-Mar-94	Died	15-Nov-94	HP			
Collun Co	17	M	A	15-Mar-94	Lived	-				
Collun Co	37	M	A	7-Apr-94	Lived	-				
Quemquentreu	30	F	A	15-Mar-94	Lived	-				?
EI Porvenir	41c	F	A	23-Feb-95	Lived	-				-
EI Porvenir	42d	F	A	10-Mar-95	Lived	-				-

* J: juvenile; A: adult

** or beginning of study period

*** PO: poison; H: hunting; FD: feral dogs; HP: poacher; DD: domestic dogs; PU: puma; U: unknown

a, b, c: indicates it is the same culpeo, before or after dispersal

d: dispersed; lc: loss of collar; t: transient; censored: left population

APPENDIX III
CAPTURE DATA AND FATE OF CULPEOS RADIO-TRACKED IN
FORMERLY HUNTED, HUNTED, AND UNHUNTED RANCHES IN
NEUQUEN BETWEEN MARCH 15, 1995, AND MARCH 14, 1996.

Ranch	No fox	Sex	Age *	Beginning of study period	Fate (until 3/14/96)	Death or censor date	Cause of death **	Dispersed to other / within ranch (hunted: H, or un hunted: UH)	Dispersal distance (km)	Reproduced (of females that lived thru rep. season) (litter size, u: unknown)
FORMERLY HUNTED										
C. Pinos	2	F	A	15-Mar-95	Censored (1s)	24-May-95				-
C. Pinos	7	F	A	15-Mar-95	Lived	-				yes (u)
C. Pinos	9	F	A	15-Mar-95	Died	28-Aug-95	U			-
C. Pinos	22	F	A	15-Mar-95	Lived	-				yes (u)
C. Pinos	38	F	A	15-Mar-95	Lived	-				no
C. Pinos	39	F	A	15-Mar-95	Censored (1s)	31-Jul-95				-
C. Pinos	44	F	A	15-Mar-95	Censored (1s)	18-Jul-95				-
C. Pinos	46	M	A	15-Mar-95	Lived	-				
C. Pinos	47	M	A	15-Mar-95	Lived	-				
HUNTED										
Cantera	28	M	A	15-Mar-95	Died	20-Aug-95	H			
UNHUNTED										
Collun Co	11	F	A	15-Mar-95	Died	15-Sep-95	U			-
Collun Co	36	F	A	15-Mar-95	Lived	-				no
Collun Co	50	F	A	15-Mar-95	Lived	-				yes (u)
Collun Co	17	M	A	15-Mar-95	Lived	-				
Collun Co	37	M	A	15-Mar-95	Died	20-Jan-96	DD			
Quemquemtreu	30	F	A	15-Mar-95	Censored (1s)	14-Jun-95				-
El Porvenir	41	F	A	15-Mar-95	Censored (1s)	5-Apr-95				-
El Porvenir	42	F	A	15-Mar-95	Died	8-Jun-95	DD			-

* A: adult

** H: hunting; DD: domestic dogs; U: unknown

1s: loss of radio signal, probably due to exhausted battery

censored: left population due to dispersal or loss of signal.

APPENDIX IV
FECUNDITY OF CULPEOS IN NORTHWESTERN PATAGONIA

Fecundity of Radiotracked Females

Radiocollared females denned between November and January of each year (Appendices I, II, and III). Number of culpeo pups observed at den sites ranged between 3 and 5 during the 1993 reproductive season (Appendix I). Litters of females 2, 19, and 22 were caught and tagged. Female 10 was killed while denning and I was unable to count the number of pups at her den, which probably died soon afterwards. Female 29 was also hunted while pregnant, so her litter size was estimated from the number of embryos in her uterus. Twenty three other litters were counted in 1992 and 1993 while attempting to tag them at dens of non-collared females (12 on C. de los Pinos and 11 on Collun Co). The intensity of field work was reduced during the 1994 and 1995 breeding seasons, so for most females I only evaluated if they denned or not. Litter size was determined only for female 11 in 1994 (Tables 2 and 3). No surviving juvenile females ($n = 6$) denned on Collun Co or previously

hunted C. de los Pinos during 1993 or 1994. Two of three adult females radiotracked in hunted C. de los Pinos bred in 1993 (Appendix I). Twelve of 16 females tracked on Collun Co and previously hunted C. de los Pinos denned between 1993 and 1995 (Appendices I, II, and III).

Fecundity of Hunted Females

Only 15 of the tracts were from females killed during the reproductive season (October through February). Nine of these females had ovaries with corpora lutea (CL). Two of these were lactating (with 4 and 2 CL) and two (with 7 and 4 CL) had 7 and 3 embryos (female # 29, the only breeding juvenile female found during the radiotracking study), respectively, in their utera. The remaining five females had three to five CL and did not show signs of pregnancy yet, probably because they were all killed during the early spring season.

Most juvenile females did not breed. The ovaries of six females killed during the breeding season had no evidence of reproductive activity. Four of these females were less than one year old, and the other two were four and five years old, respectively. Three 3-year-old females killed during the winter still had corpora lutea (4, 3, and

4, respectively) in their ovaries, suggesting that they did breed during the previous season. Eleven of the remaining 69 tracts obtained during the non-breeding season (April through September) contained growing folliculi in their ovaries, which could have developed corpora lutea. Three of these 11 tracts were from juveniles and the remaining eight were from 2 and 3-year-old females.

A mean of 4.57 ($SD = 1.27$; $n = 7$) corpora lutea was found in ovaries of ovulating females from hunted ranches. Mean litter size, based on number of embryos and corpora lutea from previous pregnancies, was 3.86 ($SD = 1.27$; $n = 7$), indicating an 84% rate of implantation.

APPENDIX V CULPEO DISPERSAL

Eleven culpeos dispersed from Collun Co and C. de los Pinos between 1993 and 1995. Dispersal was documented for all juveniles collared in hunted and unhunted ranches that survived to become one-year-olds except for two individuals (# 44 and 47, Appendices I, II, and VI). The radio-signal of #44 was lost when it was approximately 20 months old, and both foxes were radiocollared when 5 to 6 months old, so they could have dispersed before or after the study (Appendices I and II). Two one-year-old males also dispersed (Appendix I). Dispersal distances ranged between 10 and 90 km.

One of the 9 culpeos tagged as a puppy at a den site dispersed at least 85 km. It was shot during the 1995 hunting season on La Banadera ranch, close to where # 29 established its new range (Appendix I), southeast of the study area.

Four culpeos dispersed from the control ranch (Collun Co) to adjacent ranches. Adult male #15 dispersed to hunted

Corfone in 1993, females #9 and 39 dispersed to C. de los Pinos during the summer and fall of 1994, and #41 dispersed to unhunted El Porvenir ranch in 1995. Two culpeos dispersed from C. de los Pinos in 1993, one to an adjacent unhunted ranch (#30) and one to a distant hunted ranch (#28). One culpeo dispersed from C. de los Pinos to an adjacent hunted ranch (#45) in 1994. Three culpeos dispersed within the same ranch (2 in Collun Co and 1 in C. de los Pinos) in 1993.

Thus of seven culpeos that dispersed between ranches, two established new ranges on unhunted ranches and five did so on hunted ranches. Two culpeos that dispersed from Collun Co to C. de los Pinos ranch (numbers 9 and 39) were recorded as dispersers into a hunted ranch because they arrived before (February) and at the beginning (June) of the 1994 hunting season, respectively. Hunting took place on C. de los Pinos continuously during the last decades until the end of the 1993 hunting season. Thus these culpeos established new ranges on an area affected by hunting, independently of the fact that hunting stopped on C. de los Pinos in 1994.

APPENDIX VI
HOME-RANGE SIZE OF CULPEOS AND
ACCURACY OF RADIOTELEMETRY

Estimation of Home-Range Size

I determined home-range size of culpeos (Pseudalopex culpaeus) using 95% harmonic mean (HM; Dixon and Chapman, 1980) and minimum convex polygon estimators (MCP; Mohr, 1947) of program HOME RANGE. I used these estimators for comparison with Johnson and Franklin's (1994b) estimates of culpeo home ranges in Torres del Paine National Park. The kernel estimator is less biased than the HM estimator (Worton, 1995), but I decided to use the latter one to be able to compare my results to those of Johnson and Franklin (1994b). Home-range sizes of dispersing culpeos were estimated on either natal or new ranges according to where sample sizes >20 were obtained. Home-range size estimations for adults were done on an annual basis, and for juveniles were done using data obtained until November 15 of each year (midpoint of birthing season, Chapter I), when culpeos were assumed to be one-year old. Home range sizes are reported

as mean \pm standard error. Body mass, which in many species is correlated with home-range size, is reported as mean \pm standard deviation.

Annual home ranges of adult males (HM: 17.80 ± 2.12 km²; MCP: 10.27 ± 1.58 km²; $n = 7$) were larger than those of females (HM: 11.40 ± 1.14 km²; MCP: 8.23 ± 0.69 km²; $n = 16$). Differences were significant between HM estimators ($t = 2.64$; $df = 10$; $P = 0.012$) but not between MCP ones ($t = 1.18$; $df = 8$; $P = 0.136$). Home ranges of juvenile males (HM: 16.46 ± 2.39 km², $n = 4$; MCP: 10.72 ± 1.53 km²; $n = 5$) were significantly larger than those of females (HM: 7.75 ± 0.84 km², $n = 8$, $t = 3.12$, $df = 4$, $P = 0.018$; MCP: 5.89 ± 0.64 km², $n = 8$, $t = 2.90$, $df = 5$, $P = 0.017$; Tables VI-1 and VI-2). Home range estimations of juvenile culpeos were based on fall, winter, and early spring data unless otherwise indicated on Tables VI-1 and VI-2 due to death or dispersal of individuals or loss of radio signal (Chapter 2, Appendices I and II). Adult male culpeos weighed significantly more than females (11.02 ± 1.00 kg vs. 8.84 ± 0.67 kg; $t = 6.00$, $df = 18$, $P < 0.001$).

The spatial ecology of culpeo foxes in other non-protected areas of South America is unknown. Habitat use

Table VI-1. Home-range size and maximum distance moved (MDM) between radiolocations of culpeos in southern Neuquen between January 23, 1993, and March 14, 1994.

Ranch	Fox #	Sex	Age*	# locations	MDM	HM **	MCP ***	Comments
					(m)	95%	100%	
						(km2)	(km2)	
HUNTED								
C. Pinos								
	3	F	J	22	2419	5.52	3.73	Fall-HR
	26	F	J	17	-	-	-	****
	29	F	J	19	-	-	-	****
	30a	F	J	7	-	-	-	****
	4	M	J	19	-	-	-	****
	6	M	J	10	-	-	-	****
	8	M	J	7	-	-	-	****
	25	M	J	18	-	-	-	****
	27	M	J	15	-	-	-	****
	28b	M	J	8	-	-	-	****
	2	F	A	69	2617	9.29	4.96	
	7	F	A	46	3301	11.92	9.11	
	9c	F	A	4	-	-	-	****
	22	F	A	31	2919	7.76	5.34	
	5	M	A	9	-	-	-	****
	23	M	A	30	4945	21.51	11.11	Pre-dispersal
	24	M	A	48	3246	12.41	8.92	
Total				379				
Mean					3241			
SD					903			
Cantera	28b	M	J	3	-	-	-	****
Corfone	15d	M	A	12	-	-	-	****

Table VI-1--continued.

Ranch	Fox #	Sex	Age*	# locations	MDM (m)	HM ** (km2)	MCP *** (km2)	Comments
UNHUNTED								
Collun Co								
	9c	F	J	35	4915	11.12	6.73	Pre-dispersal
	13	M	J	7	-	-	-	****
	14	M	J	16	-	-	-	****
	18	M	J	24	2919	10.03	9.47	Fall-winter HR
	10	F	A	20	5062	6.27	4.89	
	11	F	A	35	4551	12.31	9.89	
	19	F	A	23	3298	5.26	4.61	
	12	M	A	14	-	-	-	****
	15d	M	A	16	-	-	-	****
	16	M	A	10	-	-	-	****
	17	M	A	37	3774	10.89	7.77	
Total				237				
Mean					4087			
SD					887			
Quemquemtreu	30a	F	J	2	-	-	-	****

* J: juvenile; A: adult

** harmonic-mean estimate of home range size

*** minimum-convex-polygon estimate of home-range size

**** no estimations due to small sample size

a, b, c, d: indicate it is the same fox, before or after dispersal.

Table VI-2. Home-range size and maximum distance moved (MDM) between radiolocations of culpeos in southern Neuquen between March 15, 1994, and March 14, 1995.

Ranch	Fox #	Sex	Age *	# locations	MDM	HM **	MCP ***	Comments
					(m)	95%	100%	
						(km2)	(km2)	
FORMERLY HUNTED								
C. Pinos								
	39a	F	J	20	4016	9.74	9.16	Post-dispersal
	44	F	J	34	3639	10.64	7.36	
	65	F	J	32	2514	6.57	5.24	Fall-winter HR
	45b	M	J	35	4207	17.57	11.23	Pre-dispersal
	47	M	J	31	4858	22.92	16.11	
	66	M	J	33	4259	15.34	10.02	Fall-winter HR
	2	F	A	74	5342	23.77	14.26	
	7	F	A	70	4006	16.27	9.58	
	9	F	A	55	4213	12.35	10.12	
	22	F	A	61	4332	12.65	10.91	
	38	F	A	26	3938	8.96	8.32	
	24	M	A	58	6295	23.69	18.69	
	46	M	A	26	3333	15.87	6.19	
Total				555				
Mean					4227			
SD					921			
HUNTED								
Aquinco	45b	M	J	3	-	-	-	****
Cantera	28	M	A	2	-	-	-	****

Table VI-2--continued.

Ranch	Fox #	Sex	Age *	# locations	MDM (m)	HM ** 95% (km2)	MCP *** 100% (km2)	Comments
UNHUNTED								
Collun Co								
	39a	F	J	10	-	-	-	****
	40	F	J	25	2372	6.97	5.91	
	41c	F	J	58	4060	6.12	5.06	Pre-dispersal
	43	F	J	43	2455	5.29	3.94	
	49	M	J	20	5942	-	6.76	
	11	F	A	71	3638	11.72	8.41	
	19	F	A	22	4097	9.14	7.22	
	35	F	A	20	2480	6.57	4.75	
	36	F	A	45	3723	12.95	8.88	
	42d	F	A	57	5801	15.27	10.42	
	12	M	A	8	-	-	-	****
	13	M	A	10	-	-	-	****
	14	M	A	7	-	-	-	****
	17	M	A	76	3900	15.06	11.56	
	37	M	A	45	6380	25.14	7.62	
Total				517				
Mean					4077			
SD					1421			
Quemquemtreu	30	F	A	2	-	-	-	****
El Porvenir	41c	F	A	3	-	-	-	****
El Porvenir	42d	F	A	9	-	-	-	****

* J: juvenile; A: adult

** harmonic-mean estimate of home range size

*** minimum-convex-polygon estimate of home-range size

**** no estimations due to small sample size

a, b, c, d: indicate it is the same fox, before or after dispersal.

and home-range size of culpeos was studied in Torres del Paine National Park in southern Chile (Johnson and Franklin, 1994b). Torres del Paine is located within the Patagonia region, but is topographically more rugged and more humid than the study area in southern Neuquen. In Torres del Paine culpeos selected Nothofagus thickets and matorral shrubland habitats where prey were more abundant and there was more cover for resting and den sites (Johnson and Franklin, 1994b). In the southern Neuquen steppe, culpeos used humid valleys to forage and slopes and rugged areas to rest and den (Diuk Wasser, 1995).

Habitat and prey productivity differences between T. del Paine and southern Neuquen may explain differences in home-range size between these areas. Annual home ranges of adult culpeos in T. del Paine were 1.5 to 2 times smaller (HM: $9.8 \pm 1.6 \text{ km}^2$; MCP: $4.5 \pm 0.6 \text{ km}^2$; $n = 15$; Johnson and Franklin, 1994b) than in Neuquen. Differences in home range size were not related to body size (McNab, 1971). Mean adult body weight of culpeos in T. del Paine ($11.65 \pm 0.78 \text{ kg}$ for males and $7.82 \pm 0.55 \text{ kg}$ for females; Johnson and Franklin, 1994b) was very similar to southern Neuquen. Small-mammal densities were similar between T. del Paine and

southern Neuquen, but density of the European hare (Lepus europaeus), the culpeo main prey in both areas, was higher in T. del Paine, where they averaged approximately 1 hare/ha (Johnson and Franklin, 1994a; Chapter 4).

Bias and Precision of Radiotelemetry Data

Most locations of culpeos in southern Neuquen could not be confirmed by sightings (Johnson and Franklin, 1994b), because culpeos typically escaped before being seen when approached by observers. Therefore, it was necessary to assess the error of bearings obtained during radiolocation of culpeos in the study area. An assistant placed 10 radio-transmitters on 10 locations on Collun Co and C. de los Pinos ranches, respectively. Locations were chosen at varying distances from trails that were visible on aerial photographs of both ranches, and spaced every 400 m along the trails to reduce the error associated with knowing the exact location of transmitters (White and Garrott, 1990). I obtained 2 to 8 bearings for each transmitter from the four stations most frequently used during radiolocation of culpeos on each ranch. I used a two-element hand-held antenna (A.T.S. Inc.), which was used during the entire study. Bias and precision of radiolocations were estimated

as the mean and standard deviation, respectively, of all differences between bearings obtained and "true" bearings to each transmitter (White and Garrott, 1990).

Ninety six bearings were obtained for error estimation. Estimated bias was -0.37° , which was smaller than the smallest unit used to measure bearings (1°). Thus sampling bias due to equipment defects or obstacles blocking or diverting signals was minimal. Average precision of bearings was 8.7° , and was similar on Collun Co (9.2° , $n = 63$) and C. de los Pinos (7.6° , $n = 33$).

The minimum level of precision recommended for radiotelemetry studies is 5° (White and Garrott, 1990). Low precision in this study could be due to the use of a two-element hand-held antenna, location of stations at low elevation compared to the dominant topographic features, and use of a low-resolution map for plotting of locations. I used a five-element Yagi antenna (A.T.S. Inc.) mounted on a truck only when attempting to radiolocate dispersing culpeos (Chapter 2), and on few occasions when I could not detect signals of some of the foxes. Use of the five-element Yagi, which probably would have resulted in higher precision of radiolocations, was reduced due to logistical difficulties.

However, the total numbers of locations used to estimate mean-maximum-distances moved by culpeos (Appendix VII) were large, ranging between 174 for Collun Co in 1993 (Table VI-1) and 555 for C. de los Pinos in 1994 (Table VI-2). Thus the accuracy of estimates of mean-maximum distances moved by culpeos is probably acceptable. Precision of density estimates based on distances moved (Appendix VII) was more likely associated with dispersion around means of maximum distances moved by different culpeos in each population. Dispersion of distances moved ranged between 22% (CV) on Collun Co in 1993 and C. de los Pinos in 1994, and 35% on Collun Co in 1994 (Tables VI-1 and VI-2). Finally, bias in estimates of distances moved resulting from bias of radiolocations was low.

APPENDIX VII
CALIBRATION OF THE SCENT-STATION METHOD AND
ESTIMATION OF CULPEO-FOX DENSITY

Introduction

Indices of population density that are not based on formal estimation models need to be calibrated to determine if they accurately reflect population sizes (Eberhardt and Simmons, 1987; Lancia et al., 1994). Calibration requires that both index values and estimates of population size be obtained for several time periods or locations. If the statistic is a constant-proportion index, regression analysis should indicate that the relationship between the population estimates and index values is linear and the intercept is 0. In this case the slope of the regression is an estimator of B for the equation

$$C = B * N$$

where C is the index, N is the estimated population size, and B is a proportionality constant (Lancia et al., 1994). If this relationship is known, population sizes can be

estimated for areas where only indices of density are available (Eberhardt and Simmons, 1987).

The scent-station method (Linhart and Knowlton, 1975) provides an index of abundance based on the proportion of stations that are visited by animals of one species over the total number of stations established. This method has been widely used to determine relative densities of carnivores (Conner et al., 1983) and study results have often been applied to make management recommendations. However, most studies have not evaluated the relationship between scent-station indices and population sizes. The only exceptions are studies of North America furbearers such as coyotes in Utah and Idaho (Canis latrans; Davison, 1981; Knowlton, 1984), bobcats (Felis rufus), raccoons (Procyon lotor), gray foxes (Urocyon cinereoargenteus), opossums (Didelphis virginiana; Conner et al., 1983), and river otter (Lutra canadensis; Robson and Humphrey, 1985) in Florida, and more recently raccoons in Tennessee (Smith et al., 1994) and bobcats in Georgia (Diefenbach et al., 1994).

Scent-station data provide frequency indices that generally are not related linearly to abundance or density (Lancia et al., 1994; Seber, 1982; Roughton and Sweeny,

1982). If this relationship is not linear, density-frequency transformations can be applied (Caughley, 1977). However, when frequency indices are less than 20%, the index-density relationship is nearly linear and untransformed indices can provide information about relative densities and rates of change of population size (Caughley, 1977; Lancia et al., 1994). Therefore, if scent-station indices are to be used for this purpose, it is necessary to determine if they reflect accurately population sizes of the species of interest and how the two variables are related.

The purposes of this study were to study the relationship between scent-station indices and population densities of the culpeo fox (Pseudalopex culpaeus), to calibrate those indices, and to estimate population densities of culpeos by two independent methods. Calibration of scent-station indices was conducted on two ranches (Collun Co and C. de los Pinos) in southern Neuquén, Argentina and the equation obtained was used to determine densities on four other ranches in the region.

Culpeo densities and scent-station indices on Collun Co and C. de los Pinos encompassed a relatively narrow range of values. I tested the performance of the scent-station index

over a wider range of densities by studying the correlation between scent-station indices and another index of abundance based on trap success. Data for this second index were available for Collun Co and C. de los Pinos and also for Catan Lil ranch, which had lower culpeo densities.

Methods

Study Area

The study area was located in the vicinity of the town of Junin de los Andes (40°S, 71°W) in northwestern Patagonia (Chapter 2). Sheep and cattle production in large ranches (8,000 to 27,000 has) are the primary economic activities. The ranches studied were chosen to represent dominant land-use types in the region. Cattle raising is the main activity at Collun Co ranch, sheep raising predominates at Catan Lil, La Papay, and Cerro de los Pinos ranches, and cattle and sheep are raised at La Rinconada and Los Remolinos ranches. Culpeo hunting pressure was low or non-existent at Collun Co and La Rinconada and high at the remaining ranches. Prior to 1994, all ranches maintained consistent management practices with respect to hunting and livestock for at least 80 years. C. de los Pinos owners sold 90% of their sheep and banned fox hunting in 1994. The

total area of these ranches was 1,420 km² (Chapter 2, Figure 2-2).

Culpeo Scent-Station Indices

Relative densities of culpeos were estimated on all ranches at the beginning of the hunting season between 1989 and 1995 using the scent-station method (Roughton and Sweeny, 1982; Chapter 2). Forty scent stations (eight lines of five stations each per ranch) were operated along all internal roads and trails of each ranch during one night in May or June of each year. Stations within a line were 0.4 km apart, and lines were at least 1.3 km apart to ensure independence among sampling units (Novaro, 1991; Roughton and Sweeny, 1982). Between 1989 and 1991, fermented egg powder (FEP) was used as an attractant and placed on a wooden stick at the center of each station (Roughton, 1982; Novaro, 1991). In 1992 through 1995, I replaced the FEP attractant by fatty acid scent (FAS, U.S. Department of Agriculture, Pocatello Supply Depot, Idaho) presented on a saturated plaster disc (Roughton and Sweeny, 1982). FAS has the same 10 fatty acids as FEP but is easier to quantify and handle (Roughton, 1982). Data were expressed as mean

percentage of scent stations visited (SSI) on hunted ($n = 4$) and unhunted ($n = 2$) ranches ± 1 SE.

Densities from Line Transects

Line transect (Buckland et al., 1993) data for culpeos were obtained simultaneously with transect counts to estimate European hare (Lepus europaeus) densities on C. de los Pinos and Collun Co ranches during 1993 and 1994 (Chapter 4). Hare transects were also conducted during 1991, 1992, and 1995, but numbers of culpeos sighted were too small to allow density estimations. Transect counts were done along four secondary roads and trails: one 14.1-km-long transect in Cerro de los Pinos, and three transects (7.3, 17.8, and 21.2-km long, respectively) on Collun Co ranch. These were the same roads where scent stations were operated. Each transect was sampled three to four times during late fall and early winter (May through July) of 1993 and 1994 for comparison with SSIs. All transects covered the main three habitat types: valleys, steppes, and slopes. Data were analyzed using program DISTANCE (Laake et al., 1993). Results are presented as mean density per ranch and year ± 1 standard error.

Minimum Densities from Captures and Radiotelemetry

Densities of culpeos were also estimated on C. de los Pinos and Collun Co ranches during the fall of 1993 and 1994, combining data from captures and radiotelemetry. Densities were estimated by dividing the number of captured animals by the size of the area sampled (e.g., area of effect of the traps; Seber, 1982). The sampled area was considered as the area enclosed by the traps plus a strip around its perimeter of width equal to 50% of the mean maximum-distance moved by the animals between consecutive observations (Wilson and Anderson, 1985). Density estimates were assumed to be minima because not all culpeos using the area may have been captured. This method was used to estimate minimum density of coyotes (Canis latrans) in Tennessee (Babb and Kennedy, 1989), and has been used extensively for small mammals (Wilson and Anderson, 1985; Brandt, 1963; Pearson et al., 1987). Babb and Kennedy (1989) used leg-hold traps and snares to capture coyotes within an area of known size and radiotracked coyotes to determine movement patterns.

Culpeos were trapped on Collun Co and C. de los Pinos ranches between January and May of 1993 and 1994 with number

1.5 padded leg-hold traps (Chapter 2; Woodstream Soft Catch, Woodstream Corp., Lititz, Pa.). Trapping was conducted on the same areas each year (Manzanal area of Collun Co and Padentrano area of C. de los Pinos; see Table VII-3 for sizes of areas), except for one additional area of C. de los Pinos (Quilquihue) where trapping was done only during 1993. Leg-hold traps ($n = 50$) were placed throughout each area at potential culpeo capture sites based on topography and evidence of culpeo use (tracks or scats; Babb and Kennedy; 1989). Traps were set for 43 to 104 days on each area (Table VII-3), and trapping was discontinued at each site when captures of unmarked culpeos did not occur for approximately 7 days. Numbers of culpeos used for density estimations were those captured plus unmarked culpeos killed during the trapping period on each area. Additionally, in 1994 I also considered culpeos radiocollared during 1993 and known to use the areas sampled in 1994.

Thirteen, 9, and 7 culpeos were captured on the Manzanal area of Collun Co and Padentrano and Quilquihue areas of C. de los Pinos in 1993, respectively. Additional culpeos were captured on the Manzanal ($n = 9$) and Quilquihue ($n = 8$) areas during 1994, when 4 and 2 culpeos

radiocollared in 1993, respectively, still used these areas. Eight unmarked culpeos were killed by hunters and domestic dogs in the areas sampled (Table VII-3).

Movement patterns of culpeos were studied using radiotelemetry data obtained while monitoring survival and dispersal between January 1993 and March 1995 (Chapter 2). Trapped culpeos were fitted with radio-collars (A.T.S. Inc.) weighing up to 5% of body mass (Chapter 2). Radiocollared culpeos that remained on Collun Co and C. de los Pinos ranches were monitored approximately twice each week during the study, while culpeos that dispersed to other ranches were monitored occasionally. Most locations were obtained during daytime. However, as culpeos in other areas are primarily nocturnal (Johnson and Franklin, 1994b), all animals were monitored once per hour during 4 to 10-hr periods during day and night in March and August of 1994 (Diuk Wasser, 1995). Recorded bearings were plotted on 1:50,000 scale IGM (Military Geography Institute, Argentina) maps; fox locations were determined and transformed into grid coordinates.

I calculated maximum distances moved from linear distances between consecutive locations for culpeos located

at least 20 times (HOME RANGE program, Ackerman et al., 1990). Johnson and Franklin (1994b) determined that 20 locations was the minimum sample size required to estimate seasonal home-range sizes of culpeos in southern Chile. Maximum distances moved by culpeos that dispersed were estimated on either natal or new home ranges (Appendix VI) according to where sample sizes >20 were obtained.

Twenty-seven and 30 culpeos were radiotracked during 1993 and 1994, respectively. A total of 1784 locations (1532 daytime, 252 nighttime) were obtained between January 23, 1993 and March 14, 1995 (Appendix VI, Tables VI-1 and VI-2). Maximum distances moved were determined for 12 culpeos in 1993 and 24 in 1994. Mean numbers of locations obtained each year were 32 for juveniles and 45 for adults.

Relation between Estimates

I studied the relationship between SSIs and culpeo densities using linear regression analysis (Sokal and Rohlf, 1995). I used a resampling regression method due to the small sample sizes ($n = 4$ ranch-years) and lack of independence among observations (Edgington, 1995). Significance of results was determined by calculating 95% confidence intervals around estimates using program

RESAMPLING-STATS (Bruce et al., 1995). Population densities on all ranches and years were calculated dividing SSIs by the slope of the regression equation between SSIs and culpeo densities.

Trap Success

The number of culpeos caught per 1,000 trap-nights was calculated using data obtained while trapping for the radiotelemetry study on Collun Co and C. de los Pinos in 1993 and 1994 (Chapter 2). Trapping data were also obtained on Catan Lil ranch during late fall and early winter of 1990 for a preliminary radiotelemetry study. Trapping on Collun Co and C. de los Pinos was done with Victor No. 1.5 soft-catch coil-spring traps (Woodstream Corp., Lititz, Pennsylvania). Trapping on Catan Lil was done with locally-available leg-hold traps that were padded with rubber to prevent injuries to culpeos and that were similar in size and clamping force to the Victor traps. Trapping in all areas was done with assistance from an experienced trapper, except for C. de los Pinos in 1993 where trapping was done without assistance. The relationship between trap success

and SSIs was studied using correlation analysis (Sokal and Rohlf, 1995). Results were considered significant when $P < 0.05$.

Results

SSIs of culpeos ranged between 2.5% and 51.5% during May-June of each year (Table VII-1). Forty-two percent of indices were smaller than 20% and 92% were smaller than 30%.

Densities of culpeos estimated from line transects ranged between 0.77 and 1.31 foxes/km² on Collun Co and C. de los Pinos, respectively, in 1993 and 1994 (Table VII-2). Standard errors of estimates were large due to small sample sizes on transect counts. There was a significant and positive linear relationship between SSIs and density estimates from transects (Figure VII-1). The slope of the regression was 0.358 [0.284 - 0.388] and the intercept, - 0.037 [(-0.064) - (0.021)] was not significantly different from 0.

Mean maximum distances moved by culpeos on Collun Co and C. de los Pinos ranches during 1993 were 4086 m (SD = 887; n = 6) and 3241 m (SD = 902; n = 6), respectively (Table VII-3 and Appendix VI). Mean maximum distances moved on the same ranches during 1994 were 4077 m (SD = 1241; n = 11) and 4227 m (SD = 921; n = 13), respectively (Table VII-3

Table VII-1. Percent of scent stations visited by culpeos on six ranches in southern Neuquén between 1989 and 1995.

Ranch				Year			
	1989	1990	1991	1992	1993	1994	1995
HUNTED							
Catan lil	7.5	2.5	2.5	2.5	5.3	2.5	23.1
La Papay	23.3	21.7	6.7	20.0	26.7	7.7	34.3
Los Remolinos	14.3	2.9	22.9	20.1	17.4	51.5	23.5
C.de los Pinos	25.7	-	25.7	14.3	42.9	35.0	34.1
Mean	17.7	9.0	14.4	14.2	23.0	24.2	28.7
SE	4.2	5.5	5.8	4.1	7.9	11.6	3.1
UNHUNTED							
Collun Co	13.3	-	28.9	21.4	24.0	25.4	25.5
La Rinconada	8.6	5.7	11.4	23.3	17.2	28.6	25.0
Mean	11.0	-	20.2	22.4	20.6	27.0	25.2
SE	2.4	-	8.7	1.0	3.4	1.6	0.2

Table VII-2. Scent-station indices, culpeo densities estimated with line transects, and trap success on three ranches in southern Neuquén.

Year-Ranch	SSI	Density (fox/km ²)	# foxes sighted	# foxes trapped	Trap-nights	Trap success
	A	B	C			D
1990						
Catan Lil	3	-	-	4	1760	2.27
1993						
C. Pinos	43	1.31 +- 0.76	16	15	4069	3.69
Collun Co	24	0.77 +- 0.50	9	13	841	15.46
1994						
C. Pinos	35	1.07 +- 0.72	12	8	445	17.98
Collun Co	25	0.82 +- 0.64	18	8	642	12.46

A: percentage of stations visited by culpeos

B: estimated with line transects

C: number of culpeos sighted on line transects

D: number of culpeos trapped per 1,000 trap-nights.

Table VII-3. Number of culpeos captured, area of effect of traps, and minimum densities on Collun Co and C. de los Pinos ranches in 1993 and 1994. MDM is the mean distance moved by radiotracked culpeos (Appendix VI).

Year-Ranch	Site	Trapping period	# foxes trapped	# foxes radio-collared & still alive in area	# foxes killed in area unmarked	Area enclosed by traps (km ²)	MDM (km)	Total area of effect (km ²)	Minimum density (ind/km ²)
1993									
Collun Co	Manzanal	11 Mar - 11 Apr	13	-	1	2.32	4.09	22.00	0.64
C. Pinos	Quilquihue	12 Jan - 26 Apr	7	-	1	1.56	3.24	12.04	0.66
C. Pinos	Padentrano	26 Feb - 31 May	9	-	3	1.32	3.24	22.55	0.53
1994									
Collun Co	Manzanal	21 Mar - 13 May	9	4	1	2.32	4.08	21.96	0.64
C. Pinos	Padentrano	18 Apr - 31 May	8	2	2	0.71	4.23	20.16	0.60

Table VII-4. Densities of culpeos on six ranches in southern Neuquén between 1989 and 1995, estimated dividing scent-station indices by conversion factor ($B = 35.8$).

Ranch				Year			
	1989	1990	1991	1992	1993	1994	1995
HUNTED							
Catan lil	0.21	0.07	0.07	0.07	0.15	0.07	0.64
La Papay	0.65	0.61	0.19	0.56	0.75	0.21	0.96
Los Remolinos	0.40	0.08	0.64	0.56	0.49	1.44	0.66
C.de los Pinos	0.72	-	0.72	0.40	1.20	0.98	0.95
Mean	0.49	0.25	0.40	0.40	0.64	0.68	0.80
SE	0.12	0.15	0.16	0.12	0.22	0.32	0.09
UNHUNTED							
Collun Co	0.37	-	0.81	0.60	0.67	0.71	0.71
La Rinconada	0.24	0.16	0.32	0.65	0.48	0.80	0.70
Mean	0.31	-	0.56	0.63	0.58	0.75	0.71
SE	0.07	-	0.24	0.03	0.09	0.04	0.01

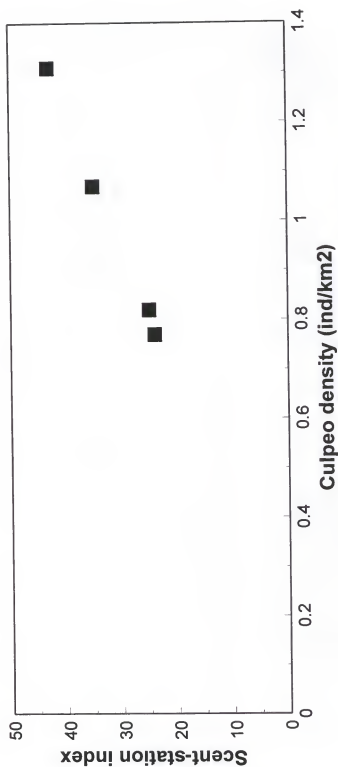


Figure VII-1. Calibration of scent-station indices (% of stations visited by culpeos) with densities of culpeos estimated with line transects on Collun Co and Cerro de los Pinos ranches during 1993 and 1994.

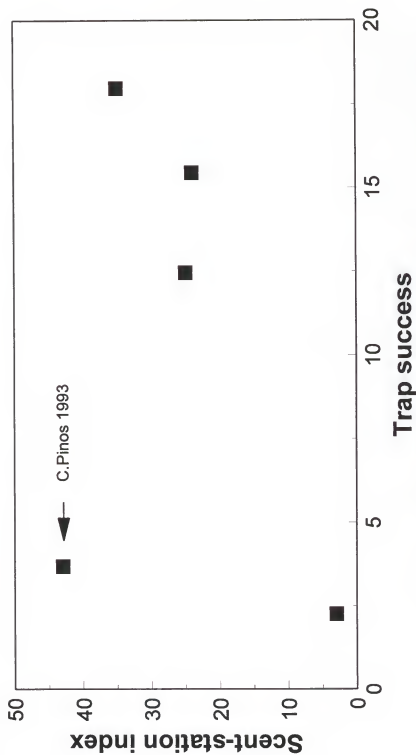


Figure VII-2. Relation between scent-station indices (% of stations visited by culpeos) and trap success (number of culpeos trapped / 1,000 trap-nights) on three ranches during 1990, 1993, and 1994. Trapping on all ranches was done with assistance from an experienced trapper, except for Cerro de los Pinos in 1993.

and Appendix VI). Total areas of effect of the traps ranged between 12.0 and 22.6 km² (Table VII-3). Minimum densities were 0.60 culpeo/km² on C. de los Pinos in 1993 (mean between Quilquihue and Padentrano areas) and 1994, and 0.64 culpeo/km² on Collun Co during both years (Table VII-3). There was no significant linear relationship between SSIs and minimum density estimates. The slope of the regression was -0.158 [(-0.391) - 0.388] and was not significantly different from 0. Thus, the relation between SSIs and minimum densities was not used.

I used the slope of the regression between SSIs and culpeo densities from transects to calculate densities on all ranches and years (Table VII-4). Densities of culpeos ranged between 0.07 foxes/km² on Catan Lil from 1990 to 1992 and in 1994, and 1.44 foxes/km² on Los Remolinos in 1994. Mean densities in the study area increased from 0.43 foxes/km² in 1989 to 0.81 foxes/km² in 1996 (Table VII-4).

The correlation between SSIs and trap success was not significant (R Square = 0.229, $P = 0.4153$) when all indices were considered ($n = 5$; Table VII-2). However, the correlation was significant (R Square = 0.9718, $P = 0.0142$, $n = 4$) when data from C. Pinos in 1993, the area where

trapping was done without the assistance of an experienced trapper, were excluded (Figure VII-2).

Discussion

Culpeo Densities

Only two estimates of culpeo density are available in the literature. Abello (1979; cited in Ginsberg and Macdonald, 1990) estimated a density of 1.3 culpeos/km² in Torres del Paine National Park in Chile using a strip census and Crespo and De Carlo (1963) estimated population density at 0.72 culpeos/km² on Campo Grande ranch in southern Neuquén Province (Chapter 2, Figure 2-2). Crespo and De Carlo's estimate was based on removals, but was not obtained with a formal density estimation method.

Culpeo densities determined from line-transects in this study were similar to those reported for Campo Grande ranch and Torres del Paine. In particular, culpeo density on an intensively hunted ranch like C. de los Pinos may be as high as that on protected Torres del Paine National Park. This relationship suggests that hunting may have little impact on culpeo densities in areas that are part of a mosaic of hunted and unhunted ranches (Chapter 2). However, this conclusion should be taken with caution. First, sample

sizes for estimating densities were low. In addition, there are other major differences than hunting between T. del Paine and southern Neuquén. For example, pumas (Puma concolor), which occur in higher densities in T. del Paine, may be predators (Chapter 2; Iriarte et al., 1991) and potential competitors of culpeos (Chapter 4). Other potential competitors like chilla foxes (Pseudalopex griseus) are common in T. del Paine (Johnson and Franklin, 1994b) but only occurred on the eastern portion of my study area (La Rinconada and C. Lil ranches). High abundances of potential predators and competitors of culpeos in Torres del Paine may explain the similarity in densities with the intensively hunted ranch in southern Neuquén.

Calibration of Scent-Station Indices

Scent-station indices seem to accurately reflect the population densities of culpeos in steppe habitat in southern Neuquén. This conclusion is based on the calibration of SSIs with densities from line transects. However, these density estimates had two main limitations.

First, estimates of density obtained with the transect method had high variability due to small sample sizes. Thus, comparison of transect estimates with minimum

estimates from captures and radiotelemetry was necessary to evaluate the reliability of the use of the conversion factor for SSIs based on transect estimates. Minimum densities were expected to be lower than transect densities because not all culpeos using the study area may have been captured. However, it is likely that a high proportion of animals in each population was trapped, because captures declined sharply in each area at the end of trapping periods. Minimum densities on Collun Co were similar to densities estimated from transects, suggesting that line-transect counts produced accurate estimates of culpeo densities on that ranch. Minimum densities on C. de los Pinos were approximately one half of densities estimated from transects. This inconsistency may be the result of trap shyness of culpeos due to previous experience (Babb and Kennedy, 1989) on C. de los Pinos, where trapping with leg-holds was intense for decades until it was banned by owners in 1994 (Chapter 2). In contrast, no leg-hold trapping was done on Collun Co before our study. Therefore, culpeos on this ranch may have been more likely to be caught with traps than on C. de los Pinos, leading to higher estimates of minimum density on Collun Co.

The second limitation of density estimates from transects was that only a small range of densities was used in the calibration due to relatively similar densities on Collun Co and C. de los Pinos in 1993 and 1994 (i.e., no SSI < 24% and no density < 0.77 fox/km² was used). However, results from the correlation between the trap-success data and SSIs suggest that scent-station indices also reflect culpeo densities accurately at low density levels like on Catan Lil ranch.

Further evaluation of the relationship between culpeo densities and scent-station indices is required to determine the reliability of these indices. In particular, a broader range of sites with lower culpeo densities should be studied. The scent-station method also should be calibrated for use on culpeo foxes in other habitat types, because the relationship between SSIs and densities is likely to be different from the one in this study (Roughton and Sweeny, 1982). This is relevant because the scent-station method is beginning to be used widely in southern South America for scientific (Jimenez, 1993; Martinez et al., 1993) and management purposes (Novaro and Funes, 1994; von Thungen, 1991).

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BIOGRAPHICAL SKETCH

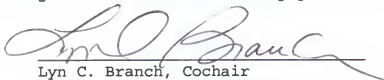
Andrés Jose Novaro was born on February 13, 1962, in Buenos Aires, Argentina. He attended the University of Buenos Aires where he obtained his Licenciado degree in biology in 1985. He began work on wildlife conservation in 1984, as a research assistant with the Argentinean National Wildlife Agency on a project on the sustainable use of tegu lizards in the Chaco. In 1987 he started work on the ecology and conservation of foxes and other wildlife in the Patagonian steppe, with a fellowship from the Research Council of Argentina. Between 1989 and 1991 Andrés earned a Master's degree at the University of Florida with a Fulbright fellowship. Thanks to support from the Tropical Conservation and Development Program and the Program for Studies in Tropical Conservation (and the University of Buenos Aires while in the field) he was able to continue on a Ph.D. at the University of Florida. In Gainesville he met his wife Susan and in the field his daughter Jimena was born, two never ending sources of joy.

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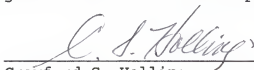
Kent H. Redford, Chair
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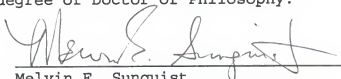
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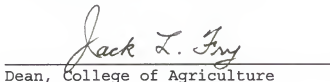


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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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